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Cover illustration: Original drawing by John Abbot (1751 ca.1840) for Plate 22 of "The Natural History of the Rarer Lepidopterous Insects of Georgia" (1797). Provided by John Calhoun, courtesy of The Sheridan Libraries, Johns Hopkins University.

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A GLIMPSE INTO A "FLORA ET ENTOMOLOGIA": *THE NATURAL HISTORY OF THE RARER LEPIDOPTEROUS INSECTS OF GEORGIA* BY J. E. SMITH AND J. ABBOT (1797)

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ABSTRACT. The illustrations for *The Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith & Abbot 1797) were reproduced from drawings by artist-naturalist John Abbot, who also supplied life history data on each species. James Edward Smith edited Abbot's manuscript and provided additional information for the book. Abbot's original manuscript entries for the 24 butterfly plates are transcribed and compared with the corresponding published letterpress. The early stages and plants in Abbot's butterfly drawings are evaluated. Eighty copies of the book were located in six countries. Dated watermarks on the plates are tabulated and plate captions are compared. Two different versions of Plates 77 and 78 are figured and discussed. Abbot's notes for Plate 31 are reproduced for the first time. A memorandum about the book by J. E. Smith is transcribed. Authorship attribution and past owners of the book are reviewed. At least one early printseller sold sets of plates without letterpress. To promote nomenclatural stability, a lectotype is designated for *Papilio bathyllus* J. E. Smith.

Additional key words: *Dasychira*, *Thorybes*, hostplants, lectotype, watermarks

Heralded by Rothschild & Jordan (1906) as "perhaps the best lepidopterological work of the eighteenth century," *The Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith & Abbot 1797) was the first major work on North American insects. It has been praised, both for its scientific merit and the quality of its hand-colored plates. It was authored by two extraordinary naturalists. James Edward Smith (1759–1828) was an English doctor and eminent botanist, who founded and served as the first President of the Linnean Society of London. John Abbot (1751–ca. 1840) was an adventuring Englishman who devoted his adult life to documenting the flora and fauna of an untamed southeastern North America. Abbot's groundbreaking artistry contributed to a revolution in entomological illustration. Regrettably, this was the only publication to acknowledge Abbot as an author.

Insects of Georgia was produced in two lavish folio volumes, measuring roughly 31 cm x 41 cm (12 in x 16 in). The entire title was cumbersome, but typical of the period: *The Natural History of the Rarer Lepidopterous Insects of Georgia, Including Their Systematic Characters, the Particulars of Their Several Metamorphoses and the Plants on which They Feed. Collected from the Observations of Mr. John Abbot, Many Years Resident in that Country.* Like other significant publications of its era, the letterpress (text) was provided in English and French in an effort to appeal to both British and continental European buyers. The French translation was allegedly provided by "Romet," who also translated the 1794 edition of "The Aurelian" by Moses Harris (Hagen 1862–1863, Horn & Schenkling 1928–1929). No expense was spared in the production of *Insects of Georgia*. The volumes were printed using the finest wove paper from England and included 104 masterfully etched and hand-colored plates of life-size figures, 24 of which depicted butterflies and 80 portrayed moths. The book was exceptional in that it included figures of larvae, pupae and hostplants of each species, not just rigid "cabinet style" illustrations of adult specimens typical of most other early entomological works. The text was subordinate and merely placed the images into the context of contemporary zoological wisdom. Smith's written descriptions were brief, relying on the figures to convey the concept of each species. American entomologist Thaddeus W. Harris wrote in 1830 that the species were "easily identified by Abbott's figures, although from Smith's descriptions alone I could not have made out half of them" (J. E. Le Conte correspondence, American Philosophical Society). The book documented Abbot's observations in Georgia from 1776 to 1792, but also some of his earlier findings in Virginia from 1773 to 1776.

Forty-three of the 57 Lepidoptera species described by Smith in *Insects of Georgia* are still recognized, having endured over 200 years of taxonomic scrutiny. In addition, plates in *Insects of Georgia* inspired Johann C. Fabricius (1745–1808) to describe six new butterfly taxa based on the figured hostplants as identified in the book. They are all replacement names for earlier taxa mostly proposed by Fabricius himself, but were not published before his death in 1808. They remained unpublished until a facsimile of this work was produced 130 years later (Fabricius 1938).

Two centuries of critical appraisals have been overwhelmingly friendly to *Insects of Georgia*. English naturalist William Jones was perhaps the first to assess

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the book in a letter to Smith dated 9 September 1797 (Smith correspondence, Linnean Society of London; transcribed in Smith (1832)). After obtaining a gratis copy that Smith arranged through a local bookseller, Jones wrote, "I took it under my arm, but soon found it sufficiently weighty...so I laboured abundantly with my load, in expectation of high gratification from the contents when I should get home—and truly I was not disappointed." He added, "upon the whole, it has the three great requisites to a modern publication,—good letter, good paper, and showy plates." Adrian H. Haworth, another of Smith's friends and later author of *Lepidoptera Britannica* (Haworth 1803–1828), described *Insects of Georgia* as "a magnificent work in folio" (Haworth 1807). English naturalist William Swainson, who was seldom complimentary, praised the book as "unquestionably one of the most beautiful and the most valuable that this or any county can boast of." He thought it was one of the two "best illustrative publications upon Insects that have ever been given to the world" (Swainson 1834). Duncan (1841) wrote, "of this magnificent publication it is not easy to speak in terms of too high commendation." Scudder (1888a) considered *Insects of Georgia* as "an epoch in the history of entomology in this country." Meiners (1948) called it "a sumptuous work characteristic of fine book printing of its day." Rare book firm H. P. Kraus ([1964]) characterized it as a "splendid example of the English color-plate book in its best period." Anthony H. Swann of the once renowned London bookseller Weldon & Wesley credited his taste for fine old books to a copy of *Insects of Georgia* that the firm had in its showroom in 1974. The bookseller described it as "the most important illustrated work on American natural history of the 18th century" (Swann 1996).

The most comprehensive review of *Insects of Georgia* was published in January 1798 by an anonymous critic who eloquently declared, "In this state of fluctuation, between the bursting of old, and the bubbling up of new theories, the greatest service that can possibly be rendered to the real progress of entomology, is the collection of the produce of judicious researches; and in this respect, the volumes before us are of the highest value. What is given here are not fragments of knowledge, but the result of a series of finished observations. If the work allure and delight by splendour of appearance, and uniform elegance of execution, it still more surprises and instructs by the richness and novelty of it's contents, the lucid order with which they are digested, the precision and vivacity of the designs, the modesty of method, and spirit of philosophy, that pervade the whole" (Anonymous 1798).

Like other contemporary works, *Insects of Georgia* included a brief excerpt of poetry that conveyed a sentiment about the subject matter. On the title page, Smith quoted two lines from a poem credited to "Mrs. Barbauld." This poem was entitled "To a LADY, With some painted Flowers" and was published by Anna Laetita Aikin (1773), who used her married name of Barbauld for later editions. Smith revealed his botanical inclinations by applying a poem about flowers to Lepidoptera.

Insects of Georgia was initially offered in 1797 in printer's boards for 20 guineas, equivalent to £21 (Bent 1799, Rich 1846, Allibone 1886). This price had the same "purchasing power" as £1,485 in 2002 (Officer 2004). Bohn (1841) listed a slightly higher original price of £25, 4s, but the £21 price is supported by a contemporary inscription in a copy of the book at Tulane University that reads "published at 21£ bds [boards]." A typesetting error is probably responsible for the ridiculously low original sale price of £2, 2s given by Anonymous (1798). A review of auction catalogs and book price indexes revealed over 40 published sales of the book dating to as early as 1815. Eleven sets have been auctioned over the last 25 years. Owing to the recent popularity of early color plate books on natural history, the value of Insects of Georgia has skyrocketed during this period. A finely bound copy sold in 1988 for $55,000 US (McGrath 1988), then equivalent to £30,900 (Officer 2004). A unique copy with vellum plates was sold in 1997 for £50,000 (Leab 1998, Heath 1999). Since the 1990s, butterflies and moths have become increasingly popular subjects of antiquarian artwork. Copies of *Insects of Georgia* are often broken in order to sell the plates individually, while the letterpress is typically discarded or presented with the plates. Unfortunately, this practice is ensuring the loss of surviving intact volumes.

Despite its great modern value, there was little market for this type of elaborate publication in Europe or America during the late eighteenth and early nineteenth centuries. Swainson (1834) estimated that nine out of ten illustrated books were sure to "entail pecuniary loss upon their projectors." Indeed, publisher James Edwards complained that he had lost money in the production of *Insects of Georgia* and had no desire to publish a continuation of the work (1806 letter from John Francillon to John Philips, British Library, London). There is evidence, however, that the book was reissued multiple times. Two plates exhibit different states (versions) between issues, leading to misconceptions about the identity of two moth taxa described in the book. Captions on the plates also vary. While researching the work of John Abbot, I became intrigued by these and other discrepancies. I embarked

upon a study to better understand the enigmatic history of this legendary publication and assess the scientific accuracy of its butterfly illustrations. I herein present the results of this investigation and offer an extended glimpse into the production of *Insects of Georgia* (Smith & Abbot 1797).

METHODS

Surviving copies of Insects of Georgia were located via WorldCat of the Online Computer Library Center (OCLC), web-based library catalogs, miscellaneous published references, and other lepidopterists. Each repository was contacted and/or visited to obtain relevant data. I personally examined the following materials: 1) 15 copies of the book in the US and UK, 2) John Abbot's original drawings and manuscript notes for the book deposited at The John Work Garrett Library of The Johns Hopkins University and the Linnean Society of London, 3) Lepidoptera drawings by Abbot at The Natural History Museum, London, as well as those at the University of South Carolina and the University of Georgia, 4) the correspondence of J. E. Smith and William Swainson at the Linnean Society of London and 5) the John E. Le Conte correspondence at the American Philosophical Society, Philadelphia. I identified the insects portrayed in the 24 original butterfly drawings for the book. Figures of larvae and pupae were evaluated for accuracy using written descriptions, line drawings, and photographs of living specimens for comparison. Digital photographs of the butterfly plates were submitted to a qualified botanist for accurate determinations of the depicted plants, which were then evaluated as valid hostplants. Specialists were contacted to verify the identities of several butterfly and moth species. Type material was examined to confirm the identity of one species of butterfly. A digital scan of an old set of 73 individual plates was analyzed and compared with plates bound into copies of the book.

RESULTS

Original drawings, notes, and a mutual friend. The nucleus of *Insects of Georgia* is a set of 104 drawings and accompanying notes by John Abbot, who left London in 1773 and lived out the remainder of his life in Virginia and Georgia. Abbot may have prepared the drawings expressly for Smith, but it is still obscure how Smith acquired them. It is doubtful that Abbot would have personally sought Smith as a potential author of a book about Lepidoptera. Smith was primarily a botanist who was only 14 years old when Abbot departed London for America. Smith more likely admired Abbot's work at the shop of John Francillon (1744–1816) and ordered a set of drawings for possible publication. Francillon was a London jeweler who sold Abbot's drawings and specimens to the naturalists of Britain and Europe. Smith was acquainted with Francillon and undoubtedly understood Francillon's unique relationship with Abbot. The purchase of the drawings through a third party is supported by the absence of letters from Abbot among the Smith correspondence at the Linnean Society of London (see Dawson 1934). At first, Smith may have been interested in the drawings solely for their botanical value. Upon receiving them he no doubt realized their greater significance, stating in the preface, "Mr. Abbot's accurate illustrations...render his farther remarks upon insects extremely desirable."

As asserted by Dow (1914), Abbot probably did not learn of *Insects of Georgia* until sometime after its publication. Smith is known to have presented gratis copies of the book, but he did not even donate a copy to his own Linnean Society until at least 1805 (Anonymous 1807a). Abbot almost surely obtained a copy of *Insects of Georgia* by about 1813, as he wrote Latin names from the book on a number of drawings he prepared for John E. Le Conte (Calhoun 2004). In 1816, Abbot directly referred to "Smith's Lepidoptera Insects of Georgia" in a letter to William Swainson (Swainson correspondence, Linnean Society of London).

The original drawings for *Insects of Georgia* were completed ca. 1783–1792. This was established from 1) Abbot's accompanying notes for Plate 18 that mention finding *Urbanus proteus* (L.) "plenty in the Year 1782, but have not seen any since," and 2) 1793 is the earliest date etched on the printed plates. As far as I could determine, no lepidopterist had examined the original drawings or notes for *Insects of Georgia* since the publication of the book.

Abbot's manuscript for these drawings is entitled, "A Natural History of the North American Insects. Particularly those of the State of Georgia. Including the changes of the principal Insects of those parts, together with the plant or flower each species feeds on, in their Natural Colours. Drawn from Nature by John Abbot many years Resident in those parts. With Notes Scientific and Illustrative." The manuscript was purchased in 1829 by the Linnean Society of London along with Smith's library and collections (Gage & Stearn 1988). It is comprised of 34 laid paper pages measuring approximately 27 cm x 16.5 cm (10.6 in x 6.5 in). Pages 9 and 10 are missing and were probably discarded by Smith as irrelevant to the book. Apparently aware that the drawings were going to Smith, Abbot wrote, "As I intended the following, I think you may still publish it as a separate work from any

other you are at present engaged in." Referring to the species depicted in his drawings, Abbot continued, "I have not preferred to describe them in any scientific manner, leaving that for you[r] superior Ablities [sic]."

It is generally believed that the biological notes in *Insects of Georgia* were copied verbatim from Abbot's manuscript (e.g. Anonymous 1798, Harris [1950], 1972). In reality, Abbot's notes were extensively edited by Smith, who wrote in the introduction of the book that he "digested" them into "some sort of style and order." Smith inserted scientific names of plants and insects, which Abbot infrequently attempted because of his limited access to scientific publications. Smith also changed some of Abbot's common names to be more consistent with European species. Although Smith wrote numerous changes directly on Abbot's manuscript, the book shows many instances where the prose was further refined. A direct comparison of Abbot's entries with the published versions reveals Smith's countless alterations (Table 1). Also included in the sections derived from Abbot are references to the occurrence of species outside Virginia and Georgia. These remarks could be used as proof that Abbot was aware of such records and even that he received specimens from those areas. For example, Anonymous (1798) stated that "Mr. Abbot informs us" that several species "have been sometimes bred from the pupa in England." The original manuscript reveals that all these comments were derived entirely from Smith.

Although Abbot briefly worked as a schoolteacher, his grammar and punctuation was notoriously uneven. Walton (1921) ascribed this to occasional lapses of a well educated person, possibly caused by a lack of contact with educated people for long periods of time or even the approach of senility. However, Abbot's spelling actually improved with age; he repeatedly employed the incorrect spelling "Catterpillers" in the notes acquired by Smith, but this was later corrected in notes for other sets of drawings. His grammar also became more refined over time, probably through his ongoing correspondence with leading naturalists of his day. Abbot considered his brief comments to be "rude notes." He was obviously more concerned with documenting his observations than being grammatically correct.

The disposition of the original drawings for *Insects of Georgia* has been misunderstood for many years. Some thought they were the set of drawings once owned by Thaddeus W. Harris. Harris obtained these drawings from English lepidopterist Edward Doubleday who had purchased them from a London bookseller in June 1839 (Scudder 1869). This set of 84 drawings of Coleoptera and Lepidoptera is dated 1830—far too late for use in *Insects of Georgia*. Scudder (1888b) and Dow (1914) attributed these drawings to an "inferior copiest," but I recently examined them and found that their style is consistent with Abbot's work and the title page is written in his hand. In 1852, French entomologist Achille Guenée mentioned *Insects of Georgia* and remarked, "I am happy to have in front of me the original drawings of this beautiful work" (translation from French) (Guenée 1852). This set of drawings was loaned to Guenée by fellow French lepidopterist Jean B. A. D. de Boisduval, who had used them for some plates in Boisduval & Le Conte (1829–[1837]). The whereabouts of these drawings is unknown, but Abbot's accompanying notes are preserved at Harvard University (see Calhoun 2004). In 1869, John Edward Gray of the British Museum wrote that "Sir James Edward Smith published a selection of the drawings of Lepidoptera" that were acquired by the museum in 1818 (S. H. Scudder correspondence, Harvard University). This claim was repeated in 1883 by Albert Gunther of the British Museum (Gilbert 1998) and again by Weiss (1936). Kirby (1897) was less certain, suggesting that "Sir James Edward Smith may have taken his selection (though apparently not in every case)" from the drawings at the BMNH. These drawings in London, now deposited at the Entomology Library of The Natural History Museum, were completed by Abbot about 1792–1812 and later bound into 17 volumes by John Francillon. Although these illustrations include many duplicates of adults and early stages in *Insects of Georgia*, none of the compositions exactly match the plates in the book. Most recently, bookseller H. P. Kraus ([1964]) advertised a set of drawings as the originals for *Insects of Georgia*. These drawings were purchased by the University of South Carolina, who reiterated their association with *Insects of Georgia* (Ridge 1966). Now preserved in the Thomas Library, a number of these drawings include penciled annotations, probably written by an agent of H. P. Kraus, that refer to plates in *Insects of Georgia*. An analysis of these drawings indicated that they were actually reproduced in Boisduval & Le Conte (1829–[1837]) (Calhoun 2003, 2004).

The drawings reproduced in *Insects of Georgia* are preserved at The John Work Garrett Library of The Johns Hopkins University, Baltimore, Maryland. They are among Abbot's best, reflecting his strong desire to prove himself through their publication. Consistent with his early work in America, Abbot figured the ventral surfaces of butterflies by portraying adults in flight with fully outstretched wings. Sometime around 1800 he settled into his more mature style of depicting adults in more natural closed-wing postures resting on

plants, often casting shadows across their perches. Though generally considered masterful, the quality of the drawings that Abbot later produced was irregular. Most were very meticulous, while others were downright clumsy (see Calhoun 2004, 2005).

The original drawings for *Insects of Georgia* were rendered in watercolor and graphite, mostly on laid paper, though ten were completed on cream colored wove paper. Many sheets of laid paper bear undated watermarks of "Taylor," or "I Taylor. These sheets were manufactured by I. Taylor who produced paper from 1746–1794 at the Basted Mill in West Kent, England

TABLE 1. Adult butterflies, early stages, and plants depicted in Insects of Georgia. Also a comparison of John Abbot's original manuscript entries against the edited letterpress (Abbot's grammar and spelling are preserved). Insect nomenclature follows Opler & Warren (2002). Adult insect figures: D=dorsal, V=ventral, m=male, f=female. Early stages: L=larva, P=pupa, a=acceptable, u=unacceptable. B&L=Boisduval & Le Conte (1829-[1837]). Status of figured hostplants (in brackets): C=confirmed, NC=needs confirmation, E=erroneous. Historical plant determinations: JES=J. E. Smith (in Smith & Abbot 1797); AWC=A. W. Chapman (in Scudder 1872). Asterisks (°) denote taxa originally described in the book.

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
1	*Papilio polyxenes* Fab. Dm, Df, La, Pa This is a very rare instance where Abbot figured an immature larva.	*Foeniculum vulgare* L. (Apiaceae) [C] JES: *Anthum foeniculum* L. AWC: "Garden Fennel" "Rue" doubtless refers to the cultivated European *Ruta graveolens* L. (Rutaceae), which is a confirmed hostplant.	*N°. 2. Black & yellow Swallow tailed Butterfly. The Catterpiller eats fennel & Rue. Changed into Chrys. 12th July. The Butterfly was bred the 20th Do. This Butterfly is frequent in Virginia, but there is none in Georgia* [see entry for Plate 3].	PAPILIO *TROILUS*, BLACK AND YELLOW SWALLOW-TAIL BUTTERFLY. The caterpillar of this species eats fennel and rue. It changed to a chrysalis July 12th, and the butterfly came forth on the 20th. It is more frequent in Virginia than in Georgia. [Smith's tentative identification of this species as *Papilio troilus* was due to a common misapplication of the original written description of *Papilio polyxenes* Fabricius, as well as that of *Papilio asterius* Fabricius, now treated as a subspecies of *P. polyxenes*.]
2	*Papilio troilus* L. Dm, Df, Vm,La, Pa	*Sassafras albidum* (Nutt.) Nees (Lauraceae) [C] JES: *Laurus sassafras* L. AWC: *Sassafras officinale* T. Nees & Ederm.	*N°.83 The Black Sassafras Swallow tailed Butterfly. Feeds on Sassafras, The Catterpiller folds a Leaf together in which it lives, changing his habitation as its food fails round it-It has a remarkable Scent, from which some calls them mellow Worms. Changed the begining of Oct. bred 10th March. One in Virginia changed 13th Oct. bred 5th April. They are frequent about the blossoms in the Spring, And as the Weather grows hotter are frequent about wet places in Yards, fords of branches &c.*	PAPILIO *ILIONEUS*, SASSAFRAS BLACK SWALLOW-TAIL BUTTERFLY. Its food is the sassafras, the caterpillar folding a leaf together for an habitation, and removing to a new one, as its sustenance around is exhausted. These caterpillars exhale a remarkable scent, whence they are sometimes called Mellow-worms. Having changed in the beginning of October, they remained in the chrysalis state till the 10th of March. One of them in Virginia changed October 13th, and the fly did not come out till April 5th. This butterfly is frequent about blossoms in the spring; and as the weather grows hotter, resorts to wet places in court-yards, fords of rivulets, &c.
3	*Battus philenor* (L.) Dm, Df, Vf. La, Pa The synonym *Papilio serpentariae* Fabricius was derived from the figured plant on this plate as identified by Smith.	*Aristolochia serpentaria* L. (Aristochiaceae) [C] JES: *Aristolochia serpentaria* L. AWC: *Aristolochia serpentaria* L.	*N° 84. The Black Snake root Swallow tailed Butterfly. Feeds on Black Snake root, Spun up by the tail 24th April changed 26th the Butterfly was bred the 4th May, Another spun up 20th June, changed 21st bred 5th July, This is one of the common Butterflies, is frequent on the peach blossoms & others in the Spring, & is likewise plenty in Virginia-These 2 species of Catterpillers has retractile horns like No 2 & seem a specific character of the Swallow tailed tailed Genus-I think I mentioned that No 2 is not in Georgia, but this is a mistake having discovered them since* [see entry for Plate 1].	PAPILIO *PHILENOR*. SNAKE-ROOT BLACK SWALLOWTAIL BUTTERFLY. One of these caterpillars was found feeding on the black snake-root, *Aristolochia serpentaria*, and attached itself to the branch by its tail, the 24th of April. Two days afterwards it changed to a chrysalis, and the fly appeared May 4th. Another spun itself up June 20th, changed 21st, and the fly came out on the 5th of July. This is one of the most common butterflies, frequently seen on the blossoms of the peach and other trees in the spring, and is no less plentiful in Virginia. The retractile horns of this caterpillar seem appropriated to the swallow-tail tribe.

TABLE 1. continued

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
4	*Eurytides marcellus* (Cramer) Dm, Vm, La, Pa The synonym *Papilio annonae* Fabricius was derived from the figured plant on this plate as identified by Smith.	*Asimina parviflora* (Michx.) Dunal or *A. triloba* (L.) Dunal (Annonaceae) [C] JES: *Annona palustris* L. AWC: *Asimina triloba* (L.) Dunal "Highland" and "Swamp" pawpaws could refer to as many as four species; *Asimina parviflora*, *A. triloba*, *A. incarna* (W. Bartram) Exell, and *A. angustifolia* Raf., all of which are confirmed hostplants.	*N° 4. Black barred Swallow Tailed Butterfly. The Catterpiller feeds upon the Papaw, both species Highland, & Swamp Papaw. tied itself up 22d May. changed the 24th Bred the 16th of June. Continues breeding all the Summer. One that changed in Autumn came out the 10th of March following. Is not very Common but much more frequent than in Virginia. Flies very Swift, frequents fruit blossoms, & often sucks damp places in Yards at which time it may be easily Taken*	PAPILIO *AJAX*. BLACK-BARRED SWALLOW-TAIL BUTTERFLY. The caterpillar feeds on the highland as well as the swamp papaw; and having tied itself up the 22d of May, changed to a chrysalis the 24th. The fly came out June 16th. It continues breeding all the summer. One that underwent its change in autumn, came out the 10th of March following. This species is not very common in Georgia, though much more so than in Virginia. It flies very swift, hovering about the blossoms of fruit-trees, and often sucks damp places in yards, when it may be easily taken. [Due to extreme confusion over the identity of *Papilio ajax* L., this name was suppressed by ICZN Opinion 286 in 1954.]
5	*Phoebis sennae* (L.) Dm, Df, Vf, La, Pa B&L Pl. 24 figured duplicate larva and pupa.	*Chamaecrista fasciculata* (Micx.) Greene (Fabaceae) [C] JES: *Cassia chamae-crista* L. AWC: *Cassia marilandica* L.	*87. American Brimstone. Feeds on the Flower figured, Spun up 30th Aug^t changed 31st bred 10th Sep^r Another Spun up 23d Sep^r. Changed 24th Bred 6th Oct. The Catterpiller is not common, It is likewise in Virginia.*	PAPILIO *EUBULE*. AMERICAN BRIMSTONE BUTTERFLY. The caterpillar feeds on this species of cassia. One of them spun itself up the 30th of August, changed the next day, and the perfect insect appeared September 10th. Another spun on the 23d of September, changed the 24th, and came out the 6th of October. This is not a common caterpillar, though found likewise in Virginia.
6	*Danaus plexippus* (L.) Dm, Vm, La, Pa The synonym *Euploea curassavicae* Fabricius was derived from the figured plant on this plate as identified by Smith (see text).	*Asclepias tuberosa* L (Apocynaceae) [C] JES: *Asclepias curassavica* L. AWC: *Asclepias tuberosa* L. "(not *curassavica*)"	*N° 1. Large black & Orange streaked Butterfly. This Catterpiller eats the Butterfly weed. the 24th April it tied itself up by the tail, & the 25th changed into Chrysalis. The 11th of May the Butterfly came out. This Butterfly is not very Common.*	PAPILIO *ARCHIPPUS*. LARGE BLACK AND ORANGE BUTTERFLY. This caterpillar eats the butterfly weed, *Asclepias curassavica*. On the 24th of April it suspended itself by the tail; changed to a chrysalis next day, and on the 11th of May the butterfly came out. It is not a very common species
7	*Danaus gilippus* (Cramer) Dm, Df, Vm, La, Pa B&L Pl. 39 figured duplicate larva and pupa.	*Asclepias amplexicaulis* Sm. (Apocynaceae)° [C] JES: *Asclepias amplexicaulis* ° Sm. AWC: *Asclepias obtusifolia* Michx.	*N° 85. The Chesnut Butterfly. Feeds on The flower figured, Changed 18th June, Bred 26th Is not very Common & I believe is not in Virginia*	PAPILIO *GILIPPUS*. CHESNUT-COLOURED BUTTERFLY. After feeding on the plant here represented, the caterpillar changed to a chrysalis June 18th, and the butterfly came forth the 26th. It is not very common in Georgia, and is I believe, not found in Virginia.
8	*Junonia coenia* (Hübner) Df, Vm, La, Pa The name *Cynthia antirrhini* Fabricius was derived from the figured plant on this plate as identified by Smith; it should be considered a synonym of *J. coenia*, not *Junonia orythia* (L.).	*Linaria canadensis* (L.) Chaz. (Veronicaceae) [C] JES: *Antirrhinum canadense* L. AWC: *Linaria canadensis* (L.) Chaz.	*N° 6. American Peacock Butterfly. Feeds upon the Flower in the Drawingb. Tied itself up 16th April changed the 18th Bred 4th May. Continues breeding 'till late in in Autumnc, This sort is common frequents damp places. bThis flower grows in Corn fields in the Spring. Ought to be of a brighter purple cIt is a common saying here Spring & fall, never Autumn .*	PAPILIO *ORYTHIA*. AMERICAN PEACOCK BUTTERFLY. Its caterpillar eats the plant here represented, which grows plentifully in cornfields in the spring. One of them suspended itself April 16th, changed the 18th, and became a butterfly May 4th. This species continues breeding till late in the autumn, and is very common, frequenting damp places. [Smith incorrectly considered this species to be synonymous with the Asian butterfly, *J. orythia*]

TABLE 1. continued

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
9	*Vanessa virginiensis* (Drury) Df, Vf, La, Pa The synonym *Cynthia gnaphalii* Fabricius was derived from the figured plant on this plate as identified by Smith.	*Pseudognaphalium obtusifolium* (L.) Hilliard & B. L. Burtt (Asteraceae) [C] JES: *Gnaphalium obtusifolium* L. AWC: *Gnaphalium polycephalum* Michx.	*N° 5. American Painted Lady Butterfly. Feeds upon Everlasting. Tied itself up 25th April. Changed the 26th Bred 8th May. Continues breeding all the Summer. One that changed the 7th May was bred the 16th. Caterpillers folds & spins the leaves together like the English sort. This Butterfly is frequent, often sucks damp places about houses.*	PAPILIO *HUNTERA*. AMERICAN PAINTED LADY-BUTTERFLY. Feeds upon the everlasting. One caterpillar tied itself up the 25th of April, changed the 26th, came forth a fly the 8th of May. Another that did not change till the 7th of May, came out the 16th. This caterpillar folds and spins the leaves together like that of the English Painted-Lady, *P. Cardui*. It continues breeding during the summer, and is very commonly seen sucking up moisture from damp places near houses
10	*Limenitis arthemis* (Drury) (ssp. *B. a. astyanax* (Fab.)) Dm, Df, Vf, La, Pa	*Vaccinium* sp., probably *stamineum* L. (Ericaceae) [C] JES: *Vaccinium stamineum* L. AWC: *Vaccinium stamineum* L. Scudder (1888-1889) thought Abbot's "Wild Gooseberry" was a species of *Ribes* L. (Grossulariaceae), but it was probably Abbot's name for the depicted Vaccinium. "Wild Cherry" (*Prunus* sp.) (Rosaceae) and "Willow" (*Salix* sp.) (Salicaceae) are confirmed hostplants.	*N° 53. Black and Blue Admirable Butterfly, The Catterpiller was taken the begining of June, feeding on the Wild Gooseberry, It also eats Wild Cherry, and Willow. The 8th June it Spun up by the tail, and the 9th changed into Chrysalis, The Butterfly was bred the 18th This Butterfly likewise breeds early in the Spring, having taken them 19th April. It is also in Virginia, but neither the Butterfly or Catterpiller is very Common. Note the figure of the Catterpiller might be a size larger.*	PAPILIO *URSULA*. BLACK AND BLUE ADMIRABLE BUTTERFLY. This caterpillar was taken early in June feeding on the wild gooseberry. It also eats the wild cherry and willow. On the 8th of June it suspended itself by the tail, and changed to a chrysalis on the 9th. The butterfly appeared on the 18th. This species also comes out of the chrysalis early in the spring; I have taken it on the 19th of April. It is not very common either in the *larva* or perfect state, though found in Virginia as well as in Georgia. The caterpillar in the plate is somewhat under the full size.
11	*Polygonia interrogationis* (Fab.) Dm, Vm, La, Pa B&L Pl. 51 figured duplicate larva and pupa. The pronounced falcate forewing tips of the adults are more consistent with the overwintering form of the species, while the overall coloring is more typical of the summer form 'umbrosa'. Lintner (1869) also noted this disparity on the published plate. The synonym *Cynthia tiliae* Fabricius was derived from the figured plant on this plate as identified by Smith (see text). Scudder (1870) described *Grapta crameri*, based in part on the adults figured on this plate.	*Tilia americana* L. (Malvaceae) [NC] JES: *Tilia alba*, Ait. Hort. Kew. AWC: *Tilia pubescens* Aiton May be a valid captive rearing, but Abbot did not figure or mention *Tilia* as a host of this species in his later drawings. "Warhew" is doubtless a misspelling of Wahoo, a colloquial name for *Tilia*. "Lime tree" is also a common name for species of *Tilia*. "Elm" (*Ulmus* sp.) (Ulmaceae) and "Sugar berry" (*Celtis* sp.) (Ulmaceae) are confirmed hostplants.	*86. American Comma. Feeds on the Warhew+ figured, Elm, & Sugar berry, Spun up 29th May, changed 30th Bred 7th June, Frequents Swamps & Oak Woods but is not very Common, The Butterfly lives all the Winter & comes forth very early in the Spring, And is likewise in Virginia. +If this was not always a low Bush or Shrub, I should take it for the Lime tree.*	PAPILIO *C. AUREUM*. AMERICAN COMMA BUTTERFLY. This feeds upon the plant called Warhew, which is very like the European lime-tree, except in being always a low bush or shrub; it eats also the sugar berry and the elm. It suspended itself by the tail May 29th, changed 30th, appeared on the wing June 7th. This species frequents swamps and oak woods, but is not very common. The butterfly lives all the winter in places of shelter, coming forth very early in the spring. It occurs likewise in Virginia. [Smith hesitantly associated this species with the Old World *Polygonia c-aureum* (L.), something he reconsidered in 1798; see Table 4.]
12	*Agraulis vanillae* (L.) Dm, Df, Vm, La, Pa	*Passiflora incarnata* L. (Passifloraceae) [C] JES: *Passiflora incarnata* L. AWC: *Passiflora incarnata* L.	*N° 3. Silver spotted Frittilary Butterfly. This Catterpiller feeds upon the Maycock[(a)]. Tied itself up by by the tail 8th July, changed into Chrysalis the 9th Bred the 17th. This species is sometimes frequent, & some Years rare to be met with. It is not in Virginia. [a]Is not this the passion flower, when ripe the pod is full of seeds, surrounded with a pale yellowish pulp. Tastes like an orange, but fainter is eaten by many people, Is a troublesome weed where it once gets any footing.*	PAPILIO *PASSIFLORAE*. GREAT AMERICAN FRITILLARY. One of these caterpillars tied itself up by the tail July 8th, changed to a chrysalis 9th, came forth in its perfect state 17th. This species is sometimes plentiful, but in some years very rare. It is not in Virginia. Its food is the maycock, *Passiflora incarnata*, the pod of which when ripe is full of seeds surrounded with pale yellowish pulp, tasting like an orange, but fainter, and is eaten by many people. The plant is a troublesome weed when it gets any footing

TABLE 1. continued

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
13	*Neonympha areolatus* (J. E. Smith)° Dm, Df, Vf, La, Pa The larva on some published plates is too brown. B&L Pl. 63 figured duplicate larva and pupa. The adults in the original drawing (and duplicate figures in another Abbot drawing at The Natural History Museum, London) appear to possess some characteristics that define the phenotype recognized by Gatrelle (1999) as the species *N. helicta* (Hübner).	*Sorghastrum secundum* (Elliott) Nash (Poaceae) [NC] JES: *Andropogon nutans* L. AWC: "Grass" Probably a natural hostplant or captive rearing.	*88. Blue spotted Ringlet. Feeds on the Grass figured Changed 22d May, bred 1st June. This Butterfly frequents the sides of Branches (or Rivulets) & is not in Virginia.*	PAPILIO *AREOLATUS*. BLUE-SPOT RINGLET BUTTERFLY. Feeds on the *Andropogon nutans*, but has not been observed in Virginia, though this grass grows there. The caterpillar changed May 22d, the fly appeared June 1st. It frequents the sides of rivulets, or branches, as they are called in America.
14	*Satyrium favonius* (J. E. Smith)° Dm, Df, Vf, La, Pa	*Quercus laevis* Walter (Fagaceae) [NC] JES: *Quercus rubra* L. AWC: *Quercus nigra* L. Smith questioned his identification of the depicted oak, writing on Abbot's original drawing, "rubra?" *Satyrium favonius* is an oak-feeder, thus *Q. laevis* is probably a natural hostplant.	*N° 9. American brown Hair Streak Butterfly. Feeds upon the forked leaf Black Jack Oak. Changed 28th April, bred the 13th May. This species is not very Common.*	PAPILIO *FAVONIUS*. AMERICAN BROWN HAIR-STEAK BUTTERFLY. Feeds on the forked leaved black jack, and other oaks. Changed April 28, came out in the perfect state the 13th of May. It is not a very common species.
15	*Celastrina neglecta* (W. H. Edwards) Dm, Df, Vf, La, Pa The larva in the book of vellum plates is more detailed than Abbot's original; John Harris probably based this rendition on the larva of the Old World *Celastrina argiolus* (L.) as identified by Smith.	*Erythrina herbacea* L. (Fabaceae) [C] JES: *Erythrina herbacea* L. AWC: *Erythrina herbacea* L. "Red Root, or redshank" surely refers to the confirmed hostplant of *Ceanothus americanus* L. (Rhamnaceae). For other drawings, Abbot identified "Red Root or redshank" as the host of *Erynnis martialis* (Scudder), which also feeds on Ceonothus.	*N° 59. Small Blue Butterfly. The Catterpiller was taken on the Wild kind of kidney Bean figured, It also feeds on Red Root, or redshank, This Catterpiller is rare to be met with & seems to be of the same Genus with the hair Streaks, It changed 16th June, Bred 25th June, The Butterfly is frequent in Georgia as well as Virginia.*	PAPILIO *ARGIOLUS*. LITTLE BLUE ARGUS BUTTERFLY. The caterpillar was taken feeding on the plant here represented; it also eats the red root or red shank, but is rarely to be met with, though the butterfly is often seen both in Georgia and Virginia. Its first change took place on the 16th of June, and the fly appeared nine days afterwards. [Smith's identification of this species as *C.argiolus* is reasonable, given that similar New World species had yet to be recognized and described.]
16	*Wallengrenia otho* (J. E. Smith)° Dm, Df, Vm, Lu, Pa The larva is not consistent with this species or the closely related *W. egeremet* (Scudder). B&L Pl. 77 figured duplicate larva and pupa	*Sisyrinchium* sp. (Iridaceae) [E] JES: *Sisyrinchium bermudiana* L. AWC: *Sisyrinchium anceps* Cav "Crabgrass" may refer to various grasses, not only the confirmed hostplant of *Digitaria sanguinalis* (L.) Scop. (Poaceae). Smith referred to its synonym, *Panicum sanguinale*.	*N° 58. Brown & Yellow Skipper Butterfly. The Catterpiller was taken in August, upon the kind of Grass figured, but is most frequent on Crab Grass. It spun the Grass together for a house like the rest, It spun up in the Grass 19th August, changed the 20th, Bred 30th Do. It is also in Virginia And the Butterfly is pretty common on Blossoms.*	PAPILIO *OTHO*. BROWN AND YELLOW SKIPPER BUTTERFLY. This caterpillar was taken upon the Sisyrinchium, but is most frequent on crab grass (*Panicum sanguinale*). On the 19th of August it spun the leaves together for a shelter, like the rest of this tribe, changed the next day, and on the 30th the butterfly came forth. It is also a native of Virginia, and the fly is not uncommon on various kinds of blossoms
17	*Atrytone arogos* (Boisduval & Le Conte) Dm, Df, Vm, La, Pa	*Echinochloa crusgalli* (L.) (Poaceae) [NC] JES: *Panicum crus-galli* L. AWC: *Panicum crus-galli* L. Probably a natural hostplant or captive rearing.	*89. Brown bordered Yellow Skipper. Feeds on the Grass figured, & Buffalo Grass. the Worms like the rest of the Skippers folds the grass together for Security. Spun up 25th July, changed the 27th Bred 4th August. I met with this Species in the Pine Woods on the North side of Briar Creek near Mill Town plantation, And have not yet seen it any where else.*	PAPILIO *VITELLIUS*. BROWN-BORDERED YELLOW SKIPPER BUTTERFLY. Feeds on the panic-grass figured, and on the buffalo-grass, at length folding the leaves together for protection. It spun itself up July 25, changed 27, came forth in its winged state August 4. This species has been found only in the pine woods on the north side of Briar Creek, near Mill Town plantation.

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TABLE 1. continued

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
17 continued		"Buffalo Grass" may refer to any number of grasses, not necessarily *Buchloe dactyloides* (Nutt.) (Poaceae), which is not a known hostplant.	[Mill Town Plantation was located in Georgia along the northeast side of Briar Creek in Screven County, just south of the Burke County line. It is now the site of Millhaven Plantation, the largest family-owned plantation east of the Mississippi River.]	[Smith's improper association of this species with *Hesperia vitellius* Fabricius led to nomenclatural confusion that lasted for over a century. Boisduval & Le Conte (1829-[1837]) later described *Hesperia arogos*, but they did not include letterpress for their figures, which could have corrected Smith's previous error.]
18	*Urbanus proteus* (L.) Dm, Vm, La, Pa B&L Pl. 69 figured duplicate larva and pupa.	*Centrosema virginianum* (L.) Benth. (Fabaceae) [C] JES: *Clitoria mariana* L. AWC: *Clitoria mariana* L. "Wild Pea Vine" apparently refers to *C. virginianum*. "Kidney beans" is a name that Abbot used for various species of Fabaceae	*N° 7. Swallow tailed Skipper Butterfly. The Catterpiller of this rare species I discovered by seeing the Butterfly lay some Eggs upon the Wild Pea Vine. The Catterpillers of all the species of Skippers folds the leaves together for safety like the English Admirable, which makes them not easy to be discovered, The 2d of July it spun up in the leaves, & changed into a Chrysalis the 4th covered with a bluish white powder like the Red Underwing. Bred 18th Augt. Only breeds in Autumn. I afterwards discovered some of the Catterpillers on the species of the Kidney beans. This Butterfly was plenty in the Year 1782, but have not seen any since.* [This is the only entry among these notes that refers to a specific year.]	PAPILIO *PROTEUS*. SWALLOW-TAILED SKIPPER BUTTERFLY. The caterpillar of this rare species I discovered by seeing the butterfly lay some eggs upon the wild pea-vine, for the caterpillars of all the species of Skippers fold the leaves together for safety (like the English Admirable, *P. Atalanta*) which makes them not easy to be discovered. On the 2d of July it spun itself up in the leaves, and on the 4th changed to a chrysalis covered with a bluish white powder, as in the Red Underwing. The fly appeared August 18. It breeds in autumn only. I afterwards discovered some of these caterpillars on another plant of the pea or bean tribe. This butterfly was plentiful in the year 1782, but I have not since met with it.
19	*Epargyreus clarus* (Cramer) Df, Vm, La, Pa B&L Pl. 72 figured duplicate larva and pupa.	*Robinia hispida* L. (Fabaceae) [C] JES: *Robinia pseudo-acacia* L. AWC: *Robinia pseudo-acacia* L. Identified by Scudder (1888-1889) as *Robinia viscosa* Vent.	*N° 54. Great Silver spotted Skipper Butterfly, The Catterpiller was taken feeding on the Wild Locust the latter end of August, It spins the leaves together for a house to secure itself from Birds, &c. like the rest of the Genus, The 5th of Sepr it spun up in the Leaves, & changed the 7th into Chrysalis, the Butterfly was bred the 10th of April following. It is also in Virginia but is not very Common.*	PAPILIO *TITYRUS*. GREAT SILVER-SPOTTED SKIPPER BUTTERFLY. This caterpillar was taken feeding on the wild locust tree the latter end of August. It spins the leaves together to secure itself from birds, &c. like the rest of this tribe. On the 5th of September it spun up in the leaves, and became a chrysalis two days after. The butterfly was produced the 10th of April following. It is also a native of Virginia, but not very common.
20	*Achalarus lyciades* (Geyer) Df, Vf, La, Pa The larva depicts a rosy form, but the coloration is too vivid on the published plates. B&L Pl. 71 figured duplicate larva and pupa. John Francillon used the unpublished name *"Papilio hedysarum"* to identify an Abbot drawing of this species at The Natural History Museum, London; it was based on Smith's hostplant name on Plate 20 in *Insects of Georgia*.	*Desmodium* sp., possibly *laevigatum* (Nutt.) DC. (Fabaceae) [C] JES: *Hedysarum paniculatum* L. AWC: *Desmodium paniculatum* (L.) DC	*N° 8. White bordered Skipper Butterfly. Feeds upon the Beggars lice (so called from the seeds sticking to people's Clothes) changed 10th July. Bred 23d. This species is common & Continues breeding most part of the Summer.*	PAPILIO *LYCIDAS*. WHITE-BORDERED SKIPPER BUTTERFLY. Feeds on the *Hedysarum* called Beggar's lice, from the seeds sticking to people's clothes. It changed to a chrysalis July 10, and to a butterfly 23d. This is a common species, and continues breeding most part of the summer.

TABLE 1. continued

Plate no.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot	Edited book entry by J. E. Smith
21	*Erynnis brizo* (Boisduval & Le Conte) (see text) Dm *Erynnis horatius* (Scudder & Burgess) or *E. juvenalis* (Fabricius) Df The larvae and pupa are basically acceptable for *Erynnis*, but not necessarily these species. B&L Pl. 66 figured duplicate larva and pupa.	*Galactia volubilis* (L.) Britton (Fabaceae) [E] JES: *Glycine elliptica*° AWC: *Galactia pilosa* Nutt. "Wild Indigo" (*Baptisia* sp.) is also an erroneous hostplant for these *Erynnis* species (see text).	*N° 57. Dingy Skipper Butterfly, Was taken on the Vine that the Catterpillar is figured Upon, It likewise feeds on the Wild Indigo &c. & folds itself in the leaves-it spun up 26th July in the leaves changed 27th And was bred the 5 August. Some that spun up in Sep. & Oct. was bred 22d March following; This is also in Virginia, The Butterfly is very Common in the Spring on Peach & plum Blossoms, It will likewise come & suck Damp places about the houses in the Yards-And the edges of running streams in the Roads &c.*	PAPILIO *JUVENALIS*. DINGY SKIPPER BUTTERFLY. Feeds not only on the plant here represented, but also on others of the same class, and folds itself up in the leaves, in which situation one of them spun itself up July 26, changed 27, and came out August 5. Some that enclosed themselves in September and October did not come out till the 22d of March following. The same insect is a native of Virginia, and in its winged state is very common in the spring on peach and plum blossoms. It will also come and suck damp places in the yards about houses, and the margins of running streams in the roads.
22	*Thorybes bathyllus* (J. E. Smith)° Dm *Thorybes confusis* Bell (see text) Df, Vf The larva is not consistent with this species; it most closely resembles the larva of *A. lyciades*. In fact, Abbot later applied this same figure to a drawing of *A. lyciades*, now at The Natural History Museum, London. The pupa is acceptable for *Thorybes*.	*Rhynchosia tomentosa* (L.) Hook. & Arn. (Fabaceae) [C] JES: *Glycine reticulata* Swartz AWC: *Rhynchosia tomentosa* (L.) Hook. & Arn. *Rhynchosia tomentosa* is a confirmed hostplant of *T. bathyllus* and, although unrecorded, probably also of *T. confusis*.	*N° 55. Brown Skipper Butterfly. This Catterpiller feeds on the Wild Bean, It folds the leaves together - for a retreat. The Skipper Catterpillers, oftentimes to secure themselves the better, spins the leaves together, to hide itself in, of some other plant that grows next to that they feed in, Which makes them the harder to find. It spun up in the leaves & changed the 11th of June, The Butterfly came out of Chrysalis the 24th It is also in Virginia, and is one of the Commonest sorts of the Skippers.*	PAPILIO *BATHYLLUS*. BROWN SKIPPER BUTTERFLY. This caterpillar feeds on the wild bean here represented, and folds the leaves together for a retreat. The skipper caterpillars, to conceal themselves the better, generally attach together with a web the leaves of some other plant growing next to that they feed on, which renders them difficult to be met with. This species changed the 11th of June. The butterfly liberated itself the 24th. It occurs also in Virginia, and is one of the most common of its tribe.
23	*Lerema accius* (J. E. Smith)° Dm, Df, Vf, La, Pa	*Wisteria frutescens* (L.) Poir. (Fabaceae) [E] JES: *Glycine frutescens* L. AWC: *Wisteria frutescens* (L.) Poir. "Indian Corn" (*Zea mays* L.) (Poaceae) is a confirmed hostplant (see text).	*N° 56. Brown Corn Skipper Butterfly. Was taken on the Vine that the Catterpillar is figured Upon in June, but is most commonly to be met with on the Indian Corn blades which it spins & folds over itself for its security, in which it is often met with changed into Chrysalis, It changed the 21st June Bred 29th Do. It is also in Virginia but is not near so common as the last described.*	PAPILIO *ACCIUS*. BROWN CORN SKIPPER BUTTERFLY. Brown Corn Skipper Butterfly. This was taken in June on the beautiful climbing shrub here delineated, but is most commonly to be met with in the chrysalis state on the blades of Indian corn, *Zea Mays*, in which it enfolds itself. It changed the 21st of June, and came out the 29th. It is also found in Virginia, but is not near so common as the last described.
24	*Pholisora catullus* (Fab.) Dm, Df, Vf, La, Pa	*Monarda punctata* L. (Lamiaceae) [E] JES: *Monarda punctata* L. AWC: *Monarda punctata* L. "Rignum" is an old colloquial name for *Monarda punctata*. "Careless" (*Amaranthus* L.) and "Lambs Quarter" (*Chenopodium* L.) are confirmed hostplants (see text).	*90. Black Skipper. Feeds on Rignum, Common and red Careless, & Lambs Quarter, folds the leaves together, Spun up in the Leaves, 18th June Bred 26th Do. Another Spun up 14 Sep & Changed 29th July bred 5th August, Spun up 14th Sep, Bred middle March, This Butterfly frequents Gardens & fields among Melon Blossoms &c. & is also in Virginia.*	PAPILIO *CATULLUS*. BLACK SKIPPER BUTTERFLY. Black Skipper Butterfly. Feeds on *Monarda punctata*, &c. spinning itself up in the folded leaves, in which state one of these caterpillars changed the 18th of June, and appeared on the wing the 26th; another spun and changed July 29, and came out the 5th of August, and a third which enclosed itself September 14, appeared in the middle of March. The butterfly frequents gardens and fields among melon blossoms, and is also found in Virginia.

(Churchill 1935, Balston 1992). Other unidentified and undated watermarks include a Britannia seal with the initials "WK" and a large Strasburg bend and lily pattern subtended by the initials "GR." These papers are undoubtedly also of English origin. Producing quality drawings in America was not without its challenges. In the "Introductory Notes" of his manuscript used for *Insects of Georgia*, Abbot wrote about the difficulties in mixing paints that retained their colors over time. He complained, "In some of my first Drawings the greens are turned blackish, owing to my then using Sap Green, I now quite discard it, & use a mixture of Gum Bouge & Indigo, but I even find that this fades some." He admitted that he fell "much short of the Originals for want of sufficient bright colours."

After their duplication in *Insects of Georgia*, all 104 original drawings were bound with letterpress into volumes of the book where they replaced the printed plates. In preparation for their insertion into these volumes, the drawings were trimmed to measure approximately 23 cm × 32 cm. Windows were cut into blank sheets of wove paper to within 3 mm of the drawing's dimensions. The drawings were then pasted over the windows with a nearly imperceptible seam. Page thickness was thereby minimized and both surfaces of each drawing remained visible. Some of the backing papers bear undated "J Whatman" watermarks (see below).

Smith penciled names and other annotations on many of the drawings, indicating that some of his names were "new." A large number of his inscriptions were later erased or trimmed off. In some cases, Smith instructed the engraver to alter figures for the published plates. On the original drawing for Plate 8, Smith inscribed, "Mr. Abbot writes this flower ought to be of a brighter purple." This statement was derived from Abbot's manuscript entry for this drawing (Table 1). Many drawings have the corresponding plate numbers written in pencil in the upper right corner. The bookbinder absentmindedly inserted the drawings for Plates 46 and 53 upside-down.

Two additional drawings by Abbot were inserted into the second volume. They are clearly not part of the same set and may have been acquired at a later date. Smith recorded these drawings as "105" and "106" on the last page of Abbot's notes, adding "No Description." The first drawing includes figures of adults, larva, pupa, and a plant. Although the adults in the drawing were portrayed as the same species, the male is *Erynnis brizo* (Boisduval & Le Conte) and the female is either *Erynnis juvenalis* (Fabricius) or more likely *Erynnis horatius* (Scudder & Burgess). They are associated with a sprig of what appears to be *Baptisia tinctoria* (L.) R. Br., an unlikely leguminous hostplant for these oak-feeding species of *Erynnis*. The figures of adults and early stages are the same as those in Abbot's original drawing for Plate 21 in *Insects of Georgia*. In reference to the drawing for Plate 21, Smith wrote on the unpublished drawing, "Same flies as 57 & therefore need not be engraved." Abbot often duplicated entire drawings or individual figures (Calhoun 2003, 2004, 2005). The second unpublished drawing depicts two figures of adult geometrid moths in a vertical format without early stages or a plant. The top figure is probably a male *Euchleana obtusaria* (Hübner). The bottom figure is a male *Prochoerodes lineola* (Goeze) (= *transversata* (Drury)). Written in Abbot's hand above the figures are the collection dates of "Sep 30." and "Mar."

Perhaps as part of their agreement, publisher James Edwards (1720–1816) acquired the original drawings from Smith. It was most likely Edwards who bound them with letterpress into volumes of the book. On a flyleaf in the first volume Edwards wrote, "These original drawings were made in America from nature during a residence of nearly 21 years." This obviously refers to Abbot's residency in Georgia, which began in 1776, 21 years before the publication of *Insects of Georgia*. Edwards ultimately presented these volumes to Mariamne (Maria Anne) Johnes (1784–1811). Edwards was a friend of her father, Thomas Johnes, publishing books for him and even lending money when necessary (Inglis-Jones 1950, Moore-Colyer 1992). The Johnes estate of Hafod (pronounced "Havod") was located twelve miles southeast of Aberystwyth, Cardiganshire, Wales.

On the verso of the English title page in the first volume, Edwards inscribed in ink, "To Miss Johnes in testimony of sincere regard from J. Edwards." Tipped-in on the same page is a three-page letter to Mariamne from her father. Addressed "Pall Mall Saturday," Thomas Johnes was apparently visiting London where he often stayed with Edwards in his Pall Mall home (Moore-Colyer 1992). Johnes wrote, "Mr. Edwards has just given you the most magnificent & beautiful present I have seen—nothing less than the original drawings of the American Insects." At the end of the letter, Johnes added, "Mr. Edwards sends his kind compts [compliments]." The letter implies that Edwards presented the volumes for Mariamne's birthday, though they had not met. Although the letter is undated, Johnes remarked that he had "heard that the Duke and Duchess of Rutland are on the point of a separation!! This not many months since they were married." John Henry Manners, 5th Duke of Rutland (1778–1857), was married on 22 April 1799 (Lundy 2004), thus these

volumes were probably presented for Mariamne's 15th birthday, around 30 June 1799. Mariamne suffered from increasingly serious physical disorders as she grew older, developing spinal disease by the time she was eleven. Edwards probably presented the volumes in hopes of lifting the spirits of his friend's ailing daughter. Mariamne was then struggling to walk without crutches and drinking "sulphurous" water as therapy (letter dated 23 June 1799 from T. Johnes to J. E. Smith, Linnean Society of London).

Some of the original drawings are badly stained from mildew. This damage was present prior to their placement into the volumes and may have occurred during their shipboard journey to England. An engraved black and white portrait of T. Johnes, dated 1810 and measuring 25.5 cm × 34 cm (10 in × 13.4 in), is pasted on the inside cover of the first volume. It may have been added by Mariamne before she died in 1811. Much of the main house at Hafod, including the bulk of Thomas Johnes' extensive library, perished in a fire in 1807 (Moore-Colyer 1992). These volumes must have been among the precious effects that were spared. They were likely shelved in Mariamne's study and not in the library wing of the house. Some of Mariamne's other books are currently deposited at the National Library of Wales.

Smith also knew the Johnes family. He met Thomas Johnes around 1793 (Moore-Colyer 1992) and later published a short book in which he espoused the estate's beauty and botanical richness (Smith 1810). Smith became acquainted with Mariamne when he visited Hafod in August of 1795 (Smith 1832). Upon their first meeting, Smith was amazed by the young girl's abilities. In 1795, Smith wrote, "Miss Johnes, though not above ten years of age, has taken a wonderful turn for botany and entomology" (Smith correspondence, Linnean Society of London). Despite their great age difference, they became very close friends, exchanging letters that included drawings and specimens of local plants and insects. Some of these plant specimens are still contained in small folded pieces of paper among the Smith correspondence at the Linnean Society. In June 1796 Mariamne thanked Smith for sending an insect cabinet already filled with insects. A year later, Smith dedicated *Insects of Georgia* to the teenage girl. He wrote, "Miss Johnes, of Hafod...When you look over this book, it will remind you of many hours we have passed together, in the practical investigation of similar objects to those which it illustrates." Mariamne died only 14 years after the publication of *Insects of Georgia* at the age of 27.

The volumes with the original drawings were likely left behind at Hafod when Mariamne's parents departed the estate in 1815 to reside at Langstone Cliff Cottage, Devon, England. It was here that Thomas Johnes died the following year. After his death, his widow expressed her gratitude to Smith; "You have been the friend of my beloved husband. The friend and kind instructor of my darling daughter" (Smith correspondence, Linnean Society of London). Soon after, Jane Johnes left Hafod, leaving all its contents, never to return. Hafod was neglected until 1832, when it was purchased by the very unpopular Henry Pelham, 4th Duke of Newcastle. When the Duke moved from Hafod in 1846, he took nearly everything of value with him, including the bulk of the books that the Johnes family owned. Some of these items were sent to London for sale (Inglis-Jones 1950, Moore-Colyer 1992). Mariamne's copy of *Insects of Georgia* was evidently disposed of at that time.

Evidence discovered at the Hargrett Rare Book and Manuscript Library, University of Georgia, confirm that the volumes of original drawings remained in England until the early twentieth century. Three bookseller advertisements, prepared during the early 1920s, were discovered in a copy of *Insects of Georgia*. They were originally received by Leonard L. Mackall (1879–1937), who served as librarian for the Wymberley Jones De Renne Georgia Library near Savannah from 1916 to 1918 (Mackall 1931). The De Renne collections, including this copy of *Insects of Georgia*, were acquired by the University of Georgia in 1938. A sales card dated "December-January, 1922–23" from bookseller Martin A. McGoff of Liverpool, England, offered the volumes of original drawings for £100. McGoff described the set as "contemporary straight-grained green morocco" and containing "The Complete Series of 106 Water-Colour Drawings...(includes two not published)." There is an inscription on a flyleaf in the first volume of this set, probably written in 1922 by McGoff, referring to the set as "Unique! The full set 106 of original paintings." The volumes were purchased from McGoff by The John Clark Co. of Cleveland, who again offered them to Mackall in February 1923 for $675. On a flyleaf of the first volume is the penciled notation "Cable Feb 10/23," probably written by McGoff to document the sale of the set to John Clark on February 10, 1923. Clark apparently also offered the set to New York City bookseller Ernest Dressel North, who then contacted Mackall in April 1923, apparently unaware that Clark had already advertised the same set to McGoff at a much lower cost: "I have just been offered a remarkable copy of Smith's 'History of the Rarer Lepidopterous Insects of Georgia," which I am venturing to call to your attention. Of course, the book itself is so well known that I need not describe it; but I give below a brief

description of the copy in question. It contains the complete series of the original water color drawings and is in contemporary straight-grain green morocco. I can sell the copy for $965.00. If I recall correctly, you are still connected to the library in an advisory capacity, and as such you may be willing to recommend this book to the library." North also peddled the volumes to John Work Garrett (1872–1942), a wealthy philanthropist and book collector in Baltimore. Perhaps to the chagrin of Mackall, Garrett purchased the copy from North sometime later in 1923 (Rogers-Price 1983). The Garrett home (Evergreen House) and its contents were bequeathed to The Johns Hopkins University in 1942. This copy of *Insects of Georgia* is still preserved in the Garrett family home, which houses the John Work Garrett Library.

As noted by prior booksellers, these volumes are ornately bound in contemporary green straight-grained morocco with gilt tooling and pink endpapers. The intricate frame style design of the boards matches books bound by London bookbinder Staggemeier & Welcher (signed examples in the British Library). L. Staggemeier and Samuel Welcher operated together in London from 1799 until 1809 (Howe 1950, Maxted 1977). The spine titles read "Smith's American Insects," which is consistent with other early copies of the book. The word "Drawings" appears near the tail of each spine. Placed above the T. Johnes portrait on the inside front cover of the first volume is a small matching green leather bookplate with gold embossed lettering that reads "John & Alice/Garrett/Evergreen House." The volumes are now kept in rigid green slipcases entitled "The Lepidopterous Insects of Georgia."

In 1816, Abbot informed W. Swainson that he was working on a set of drawings that included species not figured in *Insects of Georgia*, intending them as a "continuation of that work" (Swainson correspondence, Linnean Society of London). He was clearly familiar with the book and desired to see more of his drawings published. Swainson received the drawings in 1818, but replied that they were "not so highly finished as those must have been from which the plates in Dr. Smith's work were taken." Swainson never saw the original drawings for *Insects of Georgia*, as he was only ten years old when they were presented to Mariamne Johnes. The drawings completed for Swainson were somewhat smaller in size and many portrayed the same species as those published in *Insects of Georgia*, prompting Swainson to ask Abbot for "a fresh collection of drawings of such insects of the size of Smith's." Swainson ultimately abandoned any notion of producing a continuation of the book (Swainson 1840). The butterfly drawings in the Swainson set, currently deposited at the Alexander Turnbull Library (Wellington, New Zealand), will be the subject of forthcoming publication.

Cabinets. During the preparation of *Insects of Georgia*, Smith compared the species in Abbot's drawings with specimens and published references in England. He was unsure about the identity of the many species described in the works of J. C. Fabricius and Carolus Linnaeus (Carl von Linné). Smith wrote in the preface, "This difficulty has been overcome in a great measure by the access which has obligingly been allowed the editor to the cabinets of the British Museum, Sir Joseph Banks, the late Dr. Hunter...and the late Mr. Lee's. He added, "Most of even the new insects figured in this work may be found in one or other of the above cabinets." The collection of the renowned explorer Joseph Banks (1743–1820) is now at The Natural History Museum, London. The collection of William Hunter (1718–1783), Scottish anatomist and physician, is deposited at the University of Glasgow. The surviving specimens of horticulturist James Lee (1715–1795) are in the Hope Entomological Collections, Oxford University. All three of these collections contain numerous Fabrician types (Zimsen 1964). Smith also consulted the drawings of his friend, William Jones (?–1818), a wealthy wine merchant best remembered for his 1,500 unpublished Lepidoptera illustrations known as "Jones Icones," completed ca. 1783–1785 and now preserved at the Hope Library of Entomology, Oxford University. Fabricius described many new species from these drawings and Smith considered Jones' knowledge of butterflies as "perhaps unequalled." A decade earlier, Smith had purchased the collections of Linnaeus, affording him unique access to these type specimens. Finally, Smith compared Abbot's drawings with specimens in the "exquisite collection of Mr. Francillon, transmitted by Abbot himself." According to Smith, Francillon possessed specimens of all the new species portrayed in the drawings. Most of Francillon's surviving specimens are preserved at The Natural History Museum, London, and the Macleay Museum, University of Sydney.

Sometime after purchasing the Linnaean collections in 1784, Smith began adding more North American Lepidoptera specimens to his own holdings (Mikkola 1983, Honey & Scoble 2001). Smith's specimens, including species figured in *Insects of Georgia*, were acquired along with the Linnaeus collections in 1829 by the Linnean Society of London (Gage & Stearn 1988). References to some of these specimens are found in the copy of *Insects of Georgia* that Smith donated to the Linnean Society. In the margin of the letterpress for 56 species are penciled annotations that read, "In Mus.

Smith" ("In the Museum, from Smith"), "Kind in Mus. Smith," or "In Mus, Smith Specimen." The sexes of the specimens and additional remarks in Latin are sometimes also included. They refer to Smith's specimens in the Linnean Society collection, but are not in Smith's hand and were apparently written after the book was donated to the Linnean Society. Some of Smith's surviving Lepidoptera specimens at the Linnean Society are labeled "Georgia." Honey & Scoble (2001) listed a specimen of *Agraulis vanillae* (L.) that is labeled "Georgia Abbot." Other Lepidoptera specimens from Georgia are labeled "WJH" or "WJH, 1806." These undoubtedly refer to Sir William Jackson Hooker (1785–1865), a leading English botanist who later served as the Director of the Royal Botanic Gardens, Kew. It was Smith who likely directed Hooker toward a career in botany (Anonymous 1867). Hooker's Georgia specimens were probably also collected by Abbot.

Smith did not mention in the introduction of *Insects of Georgia* that he personally possessed any of the figured species, thus he probably acquired them after the book was published. He seems to have based his descriptions on a combination of Abbot's drawings and specimens in other collections. The specimens that Abbot figured, though probably lost, represent syntypes of the taxa described by Smith. Other syntypes may exist among the surviving collections that were examined by Smith, but they are almost certainly unrecognizable.

Publication. During the 1780s and 1790s, the first of the finely illustrated books began to appear from London, helping to put England to the forefront of European printing (Maxted 1977). Many London publishers during this period also maintained their own bookshops and some were also bookbinders. Dow (1914) claimed that Smith bore the expense of publishing *Insects of Georgia*, but evidence indicates that the publishers also suffered losses when the book underperformed. Publishers routinely offered authors a single payment for the copyright of a promising work (Besterman 1938). Although they operated separately, booksellers often combined their efforts to take shares in ambitious projects (Maxted 1977). *Insects of Georgia* was published by three London booksellers who organized printing, distribution, and sales. These firms also worked together on other projects and for a time after publication may have retained exclusive rights to selling *Insects of Georgia* out of their own bookshops.

James Edwards was a bookseller and bookbinder trading under the name of J. Edwards from three addresses on Pall Mall in London from 1784 until his retirement in 1804 (Maxted 1977). Edwards was the primary publisher of *Insects of Georgia* and complained to John Francillon that he had lost money in its publication. Edwards' bookshop was a popular gathering place for celebrities in the book trades (Inglis-Jones 1950). Smith may have been introduced to Edwards through their mutual friend, Thomas Johnes. John White (1765–1855) was a less influential bookseller who was located at 63 Fleet Street in London from 1792–1816. During most of this time, he traded under the name of J. White (Maxted 1977). White's business practices were reputed to be rather despicable at times (Moore-Colyer 1992).

The Cadell bookselling firm had a long legacy, being described as "the first in Great Britain and perhaps in Europe" (Timperley 1839). Thomas Cadell retired in 1793, giving the business to his son, also named Thomas Cadell (1773–1836). The elder Cadell appointed his apprentice, William Davies (?–1820), as a partner to his son. Davies initially managed company affairs, with the younger Cadell taking little interest in the trade. In 1801, Cadell & Davies sold 740 book titles to the United States government for the fledgling Library of Congress (Bisbort & Osborne 2000). Cadell took over primary management of the firm when Davies fell ill in 1813 (Besterman 1938). The firm operated under the name of Cadell & Davies until the death of Davies in 1820, after which it was known simply as Thomas Cadell. Cadell died in 1836. Cadell & Davies was located at 141 Strand and was considered among the top two or three publishers in London (Besterman 1938, Maxted 1977). The firm was sometimes accused of engaging in projects that were too ambitious and expensive. *Insects of Georgia* was probably one such risky endeavor.

Thomas Bensley II (1760–1835) was retained as the printer for *Insects of Georgia*. The firm operated under the name of T. Bensley and was located on Fleet Street in London beginning in 1785 (Maxted 1977). Tragically, the company's warehouse was destroyed by fire in 1807 and the printing office burned in 1819. Bensley reopened in 1820 at another location on Fleet Street and continued to operate until 1835 (Todd 1972). Bensley, one of London's leading printers, boasted that English presses could "rival and even excel the finest works" of continental European printers. He was one of three London printers who first became involved in the steam printing press (Handover 1960). Bensley was also the printer of richly illustrated books on insects by Edward Donovan in 1798 and 1800. Although published in a smaller format, the overall layout of Donovan's books bears a striking resemblance to *Insects of Georgia*.

Smith reorganized the haphazard arrangement of Abbot's drawings to present them in Linnaean

taxonomic order. In his "Introductory Notes," Abbot admitted that he did not "marshall them in any Order." This new arrangement was a challenge for Bensley. Blue check-marks, possibly made by Bensley, are present on Abbot's manuscript to the left of the names for each entry. Despite his care, he mistakenly transposed the notes for one of the drawings (see below). Each letterpress leaf (English recto and French verso) treated a single "Tab.," from the Latin "Tabula" (a painting, print, or plate). For the first two pages of plate letterpress, Bensley placed a comma after the Latin insect name, but curiously changed his mind and used a period for the remainder of the text (Table 1).

The title page of *Insects of Georgia* is dated 1797. Nonetheless, Sabin (1868) listed the publication date "1796–1798," which Eames (1892) interpreted as evidence that the work was "issued in numbers" to subscribers. However, a letter written in September 1797 refers to the completed book and a critical review of the entire work was published in January 1798. Thompson (1975) reverted back to 1797 in his revision of Sabin (1868). I have located 80 surviving copies and none include wrappers or other evidence of being issued in parts.

Before the days of mass production, it was customary that books were offered in simple paper-covered printer's pasteboards (laminated paper) with a label identifying the title. The buyer later chose a permanent binding in whatever style they preferred. Copies of *Insects of Georgia* were bound by such esteemed London bookbinders as Christian S. Kalthoeber and Henry Walther, as well as Joshua Devoy of Dublin. Many copies were bound in straight-grained morocco skins of red, blue or green, which were common colors of the period (Ramsden 1956). The color plates were typically bound into the letterpress along their right margins. Nonetheless, one copy I examined had the plates bound along their left margins. Other liberties were occasionally taken, such as moving the French preface to the second volume. Sometimes the French title page was even discarded. Bookbinders also frequently disagreed on where to separate the two volumes; I found some copies with as many as 54 plates in the first volume. The copy with the original drawings assembled by publisher J. Edwards includes 50 plates in the first volume, implying this was the intended layout. The copy that Smith donated to the Linnean Society of London likewise includes 50 plates in the first volume. Some owners combined their sets into a single unwieldy volume. In rare instances, bookbinders inserted some plates in the wrong order. This error appears to have been caused by confusion resulting from the lack of inked numbers on some of the plates. To help rectify this, numerals were occasionally penciled in.

Misplaced notes. Thomas Bensley confused the notes for Plates 31 and 43. Abbot's manuscript entries for these plates are consecutively numbered 66 and 67. Because of similar sentences at the beginning of these entries, Bensley mistakenly transposed most of the comments for Plate 43 into the letterpress for Plate 31. Plate 31 portrays *Proserpinus gaurae* (J. E. Smith), originally described in *Insects of Georgia* as *Sphinx gaurae*. As a result of Bensley's error, Abbot's notes for this species have never been published. They read (with Abbot's grammar and spelling preserved), "Olive shaded Sphinx. Was taken feeding on the flower figured on the Drawing in May, The 1st of June it went into the Ground, was bred the 25th. Also went in the Ground 7th Septr. Bred 27th March. Is not in Virginia, & is not very common, It flies in the Day time & sucks the blossoms of the Wild Honeysuckle."

The plates. Up to one-half of early illustrated books consisted of color plates (Swainson 1834) and *Insects of Georgia* was no exception. With 234 total printed pages and 104 plates, 44 percent of its bulk was comprised of plates. Although generally referred to as engravings, the plates in *Insects of Georgia* are etchings, which are more tonal in character. Stipple techniques were employed to create subtle shading. The platemark impressions left on the paper reveal that the etched copper plates measured approximately 29 cm × 38 cm (11 in × 15 in).

Swainson (1840), Walton (1921), and Weiss (1936) identified the primary engraver as the famed English naturalist Moses Harris (1730–ca. 1788). However, many plates clearly possess the signatures "Jn° Harris Sculp" or "J Harris Sculp" ("Sculp" is short for the Latin "Sculpsit," meaning "carved by" or "engraved by"). Not only did Moses Harris typically sign his plates "Mos Harris" or "Ms Harris," he died about five years before the first plates for *Insects of Georgia* were etched. The plates were presumably created by John Harris (1770?–1834), who has been described as an engraver, lithographer, watercolor artist, aquatintist, and miniature painter (Williamson 1919, Mallalieu 1976, Klimt & Steppes 1999–2000). He also specialized in illustrations of birds and insects (Bénézit 1966). Harris should not be mistaken for an earlier British painter, nor booksellers and publishers of the same name that were active during the late eighteenth and early nineteenth centuries. Although other published sources did not provide Harris' date of birth, the Witt Library (1978) listed it as 1770. If correct, he was 23–25 years old when he etched the plates for *Insects of Georgia*.

Harris' signature is present on many of the plates, but only some are dated. Signatures were etched along

stems or on leaves of the illustrated plants on nearly 50 plates, a few well hidden within the designs. Many other plates bear Harris' signature towards the foot of the sheets and some of these are barely perceptible. Plates with foot signatures were the earliest to be etched, being dated 1793 and 1794. One is dated "Jany 1794" and two are dated "Feby 1794." Later in 1794, Harris moved his signature into the designs. Four design signatures are dated 1794 and 12 are dated 1795. Harris' signature was printed backwards on 19 plates. One is dated 1794, while the remainder are dated 1795. Like other engravers of his era, Harris perhaps ultimately settled for more accurate signatures on the copper plates, rather than more poorly executed printed versions that were etched in reverse (Gascoigne 2004). The Sphingidae were the first plates to be etched, while most of the butterflies were among the last. The plates were randomly etched, apparently reflecting the whims of Harris alone.

Plate 16 includes a cryptic engraver's signature, "S/PAR," followed by the year 1795. The "S" is subtended by the other letters and the "P" is laterally inverted. Rogers-Price (1983) interpreted the signature as "S/IAR," but under magnification the letter on the lower left more closely resembles an inverted "P" or even a stylized "R." I was unable to identify this engraver despite consulting definitive published references and sending digital photographs of the signature to specialists at the British Museum, Smithsonian Institution, and elsewhere. There were numerous engravers active in London during the late eighteenth century (Maxted 1977). This plate was probably the very last to be etched in 1795. John Harris may have been unable to complete the work or overlooked this composition among Abbot's drawings. Not only was this plate etched by a different engraver, Abbot formatted the original drawing like his bird illustrations, with a hint of groundcover beneath the plant. The engraver further embellished the composition with a whimsical landscape that incorporated a distant building and palm trees.

The etchings for *Insects of Georgia* are meticulous and effectively capture the minute details of Abbot's drawings. There are few instances where the layout of the prints differ from the original drawings and most merely involve slight relocations of figures. The adult moths on Plates 77 and 78 were transposed on some impressions (see below). An upper flower appearing on the original drawing for Plate 33 was etched, but for some reason it remained uncolored on nearly all the finished prints—there were even attempts to erase its ink outlines. The coloring of prints for fine illustrated works was customarily entrusted to local artists or art students. Engravers sometimes colored their own prints, but I found no evidence that this was true for all copies of *Insects of Georgia*. As noted by Swainson (1840), high quality books were usually colored by "skillful hands." Despite the likely use of more talented colorists for *Insects of Georgia*, Bohn (1865) and Sabin (1868) complained that some copies were "indifferently" or "badly" colored and of less value. Walton (1921) agreed that "some of the figures have not fared so well at the hands of the colorists." I personally observed pronounced differences in the quality of plates, even within the same volumes. After coloring, many figures on the plates were heightened (varnished) with a solution of gum arabic to impart a bright, glossy appearance.

From the very beginning, there were criticisms that some of the figures in *Insects of Georgia* were imprecise. In 1797, William Jones wrote to Smith, "Sir, the merit is yours. The demerit attaches to the engraver and colourer, for there are some faults." John E. Le Conte, who would later co-author his own illustrated book based largely on Abbot drawings, wrote in 1830 to T. W. Harris about the difficulty in accurately determining "what Smith meant by many of his species [because] his descriptions are so short and many of his figures inaccurate" (Harris correspondence, Ernst Mayr Library of the Museum of Comparative Zoology, Harvard University; microfilm at American Philosophical Society). Lowndes (1834) and Brunet (1865) likewise claimed that the plates in *Insects of Georgia* were not accurate. Strecker (1872–1878) accused the colorists of performing "some funny work" and complained that the adult moth figures on Plate 29 had "no foundation except in the fancy of the person who colored the plates, who doubtless imagined that a little variety introduced would improve the natural plain appearance of the insect." A comparison of published prints for Plate 29 against Abbot's original drawing of *Laothoe juglandis* (J. E. Smith) does indeed show a deviation. The moths on the published plates have brown or reddish-brown forewings with paler yellowish-brown hindwings. Abbot's original figures have less contrasting lighter brown forewings and hindwings. Several other plates show similar deviations in color. As with any early illustrated book, the original drawings are generally more accurate and lack the vicissitudes of subsequent print colorists.

Vellum plates. A most extraordinary copy of *Insects of Georgia* is preserved in the Hargrett Rare Book and Manuscript Library, University of Georgia. The plates in these volumes were printed with black ink on vellum and 15 were signed in pencil "J Harris Pinxt" by engraver John Harris. Harris apparently colored these

prints himself and their quality is far superior to all others, even surpassing that of Abbot's original drawings. Harris imparted a three-dimensional look to the wings of the adult figures and enriched the colors with more vivid tones. The general coloration of the vellum prints is more similar to those in other copies of the book than to the original drawings, suggesting they were created after the drawings were disposed of in 1799. This is supported by the presence of 1801 watermarks on many sheets of white wove paper that were bound into the volumes to protect the vellum plates. The volumes are ornately bound in contemporary red morocco with spine titles that read "Abbot's American Insects." Like the volumes that contain the original drawings, this set was probably bound by Staggemeier & Welcher (Heath 1999) (the binder's ticket was removed from the inside cover of the first volume). The volumes are now protected in a rigid black case that identifies them as "Insects of Georgia/J. Abbot/Printed on Vellum." A penciled note on a free endpaper at the back of the second volume reads, "From the library of Prince Golitzin (see item #303 in 1866 catalogue)." Russian Prince Mikhal Aliksandrovich Golitsyn (1804–1860) was a famous bibliophile who amassed a rich library of early printed books. The faded remnants of Golitsyn's large oval bookplate are visible on a flyleaf of the first volume. A copy of *Insects of Georgia*, presumably the vellum set, was listed in the Golitsyn library catalog (Gunzbourg 1866). Additional bookplates reveal that these volumes changed hands at least three more times. Owners included English school governor Joseph Neeld (1800–1856), antique collector and publisher Moncure Biddle (1882–?), and art collector Mildred Barnes Bliss (1875–1969). The Bliss library served as the foundation for the Harvard University Dumbarton Oaks Research Library (Washington, D.C.). Dumbarton Oaks owned the vellum copy of *Insects of Georgia*, but it was discarded with other butterfly books by a former librarian who considered them to be peripheral to their collections (L. Lott pers comm.). Fortunately, the University of Georgia acquired this historic set in 1998 from the prominent New York City bookseller Donald A. Heald (Heald 2002–2005).

Larvae and pupae. William H. Edwards (1894) complained, "Abbot's figures, especially of larvae and pupae, are bad as can be." Although Edwards' assessment was based solely on engraved reproductions in Boisduval & Le Conte (1829–[1837]), some of Abbot's original figures of larvae and pupae are equally abysmal. The majority of Abbot's Lepidoptera immatures are accurate, probably having been sketched from living individuals that he reared. Larvae that are correct in form, yet improperly colored, were possibly derived from inflated (blown) specimens that he was known to provide to interested naturalists. Other figures possess conflicting characters or do not resemble any known species. These seem to have been taken from memory or contrived for the sake of the compositions. For example, the larva that he included in several drawings of *Asterocampa clyton* (Boisduval & Le Conte) is not consistent with any known species, especially *Asterocampa* (Calhoun 2004). As Abbot's knowledge became more sophisticated, he often included more accurate renditions of larvae in his subsequent drawings.

Using a number of published and unpublished references, including Allen et al. (2005) and Wagner (2005), I assessed the accuracy of the early stages depicted on the butterfly plates in *Insects of Georgia* (Table 1). Because variation is expected to occur on the published plates, Abbot's original drawings were also consulted. Except for a few minor departures in color, the published figures do not differ significantly from the originals. Abbot's duplicate figures of the larva and pupa of nine species were published in *Insects of Georgia* and Boisduval & Le Conte (1829–[1837]) (Table 1).

The Plants. Haworth (1807) emphasized the botanical relevance of *Insects of Georgia* when he wrote, "the whole Plants as well as Insects being scientifically delineated and described, that this publication is to the full as valuable to the Botanist, as it is to the Entomologist: we never before beheld the sister sciences walk so closely, and so engagingly hand in hand, as in this interesting volume.—It is truly a Flora et Entomologia." Rich (1846) agreed that *Insects of Georgia* was a valuable tool for botanists. In December 1812, botanist Stephen Elliott traveled to Columbia, South Carolina to consult a copy of *Insects of Georgia* in preparation for his landmark treatment, *Sketch of the Botany of South-Carolina and Georgia* (Elliott 1816–1824) (Ewan 1971). Evidence indicates that this is probably the same copy now deposited in the Thomas Cooper Library, University of South Carolina.

Very few early entomological illustrators portrayed hostplants and immature stages of Lepidoptera. Notable exceptions were Maria Sibylla Merian (1647–1717), Eleazar Albin (*fl.* 1690–1742), Benjamin Wilkes (*fl.* 1690–1749), Edward Donovan (1768–1837), and Moses Harris. Many of Abbot's drawings, including all those for *Insects of Georgia*, combined plants with the adults and immatures of insects. Abbot maintained that he was not a botanist, "only an admirer of Natures Beauties, to meet with a new growing flower or plant much pleases me" (Swainson correspondence, Linnean

Society of London). After a lifetime of rearing larvae on countless plants, his view of botany remained unpretentious. In a letter he wrote to T. W. Harris at the age of 84 he again professed, "I am no Botanist...there is a great variety of flowers in Georgia...I am always much pleased, when I meet with any that is new to me" (Dow 1914).

Despite arguments that Abbot's early botanical renderings were not precise (e.g. Rogers-Price 1983), the plants in his drawings for *Insects of Georgia* are essentially accurate (Britten 1898, M. A. Garland pers. comm.). They are much improved over the hostplant drawings that he completed in London prior to 1773. Abbot illustrated several North American plants for the first time among the drawings for Smith. From these, Smith proposed six new plant taxa in *Insects of Georgia*. Smith confused some other species, such as the milkweed in Plate 6, which he identified as *Asclepias curassavica* L. (Apocynaceae). This plate also portrays the butterfly *Danaus plexippus* (L.). *Euploea curassavicae* Fabricius, a proposed replacement name for this insect, was derived from Smith's identification of the illustrated plant; "Habitat in Americanae meridionalis Asclepiade curassavica" (Fabricius 1938). Smith's determination also misled Ewan (1985), who supposed this exotic plant was firmly established in Georgia by the 1790s. The illustration actually portrays the native butterfly-weed, *Asclepias tuberosa* L. (Apocynaceae).

Botanist Alvan W. Chapman, author of *Flora of the Southern United States* (Chapman 1860), identified the plants figured on the 24 butterfly plates of *Insects of Georgia* (Scudder 1872). Table 1 presents his determinations, as well as current interpretations and nomenclatural updates by Mark A. Garland (Botany Section, Florida Dept. of Agriculture & Consumer Services, Division of Plant Industry). The original identifications of Smith are also given in Table 1. Historical determinations are provided in their original nomenclature. Because of the book's botanical significance, The Missouri Botanical Garden has digitally reproduced their volumes of *Insects of Georgia* and made them available for viewing on the Internet (MBG 1995–2005).

Artist-naturalist Titian R. Peale (1799–1885) met Abbot in 1818 and related to lepidopterist William H. Edwards in 1864 that "caterpillars of all sorts were brought in [to Abbot] by negro boys in Savannah, and he generally only learned what species they belonged to when the butterfly or moth came from the chrysalid or pupa" (dos Passos 1951). Peale was mistaken, as Abbot often wrote of personally collecting larvae and watching females lay eggs to discover the hostplants (Table 1). Most plants portrayed in his American Lepidoptera drawings have been confirmed as valid hostplants. However, it is well known that some of his associations are erroneous. Over 150 years ago, Guenée (1852) observed that Abbot's plant figures "form a pleasant collection to the eyes, but sometimes do not have the least relationship with those that really nourish the caterpillars" (translation from French). Abbot may have misinterpreted his observations or intentionally figured inappropriate hosts.

Some incorrect hostplant associations were likely based on Abbot's confusion of different species. The drawing for Plate 21 depicts two species (as one) of oak-feeding skippers, *Erynnis brizo* (Boisduval & Le Conte) and either *E. juvenalis* (Fabricius) or *E. horatius*. The plant was described by Smith in the book as a new species, *Glycine elliptica* Smith (Fabaceae), now considered to be a synonym of *Galactia volubilis* (L.) Britton. This plant was also figured in an Abbot drawing used for Plate 65 of *E. brizo* in Boisduval & Le Conte (1829–[1837]) and in an unpublished drawing of *E. juvenalis* in The Natural History Museum, London. In his notes for various *Erynnis* drawings, Abbot referred to "Wild Indigo," presumably a species of *Baptisia* (Fabaceae) (Table 1). This is reinforced by the sprig of *Baptisia* figured in Abbot's unpublished *Erynnis* drawing owned by Smith. Yet another leguminous plant, *Indigofera caroliniana* Mill., is portrayed in an Abbot drawing of *E. brizo* in The Natural History Museum, London. *Erynnis zarucco* (Lucas) and *Erynnis baptisiae* (Forbes) feed on these legumes and occur in the portions of Virginia and Georgia that Abbot explored (Opler 1995), but were not recognized as different species until long after his death. Like many lepidopterists of today, Abbot often had difficulty differentiating the *Erynnis* he encountered. Abbot applied the same figures of early stages to at least three different *Erynnis* species over the years.

Abbot probably reared the larvae of many species in captivity without prior knowledge of their hosts by forcing them to accept plants that are not fed upon in nature. A forced captive rearing is probably responsible for Abbot's drawing of *Atrytone arogos* (Boisduval & Le Conte) with the unconfirmed, yet conceivable, host *Echinochloa crusgalli* (L.) (Poaceae) for Plate 17 of *Insects of Georgia*. The portrayal of *Polygonia interrogationis* (Fabricius) with *Tilia americana* L. on Plate 11 may also be the result of a captive rearing. Fabricius proposed a new name for this butterfly, *Cynthia tiliae*, based on Smith's identification of the plant on this plate; "Habitat in Americae borealis Tilia alba" (Fabricius 1938). Additional butterfly taxa named by Fabricius (1938) from the hostplants in *Insects of*

Georgia are listed in Table 1.

Regardless of Abbot's abilities, some of his hostplant relationships are simply untenable. His drawing of *Wallengrenia otho* (J. E. Smith) for Plate 16 of *Insects of Georgia* includes a species of blue-eyed grass, *Sisyrinchium* L. (Table 1). Although *W. otho* feeds on grasses (Poaceae), *Sisyrinchium* is not a grass at all, but a member of the irus family (Iridaceae). Abbot's drawing for Plate 23 illustrates the grass-feeding *Lerema accius* (J. E. Smith) with a spectacular blooming branch of the legume *Wisteria frutescens* (L.) Poir. (Fabaceae). The drawing for Plate 24 suggests another implausible association of *Pholisora catullus* (Fab.) with the mint *Monarda punctata* L. (Lamiaceae). *Pholisora catullus* feeds on members of the Amaranthaceae and Chenopodiaceae. Probably in an attempt to verify Abbot's hostplant, Scudder (1888-1889) noted that larvae of *P. catullus* refused to eat a related species of *Monarda*. These three butterflies and their natural hosts are essentially dull and unattractive. In these instances, it seems that Abbot's desire to create appealing compositions transcended his pursuit for accuracy as a naturalist. Such artistic license was not uncommon in entomological art of the eighteenth and early nineteenth centuries. Dutch naturalist M. S. Merian also made "aesthetic decisions" for her drawings that deviated from her own observations (Wettengl 1998). Abbot probably assumed that occasional alterations were necessary to satisfy his customers. The definition of Merian's work by Dance (1978) could just as easily apply to Abbot: they "combined science and art in equal proportions, meeting the demands of art at the expense, when necessary, of science." I have attempted to evaluate the validity of the hostplants in Abbot's butterfly drawings and their accompanying notes for *Insects of Georgia* (Table 1). This was done using numerous references, including Robinson et al. (2002), but was complicated by the perpetuation of unconfirmed reports in the literature. Some of these were undoubtedly derived from the very same records of Abbot.

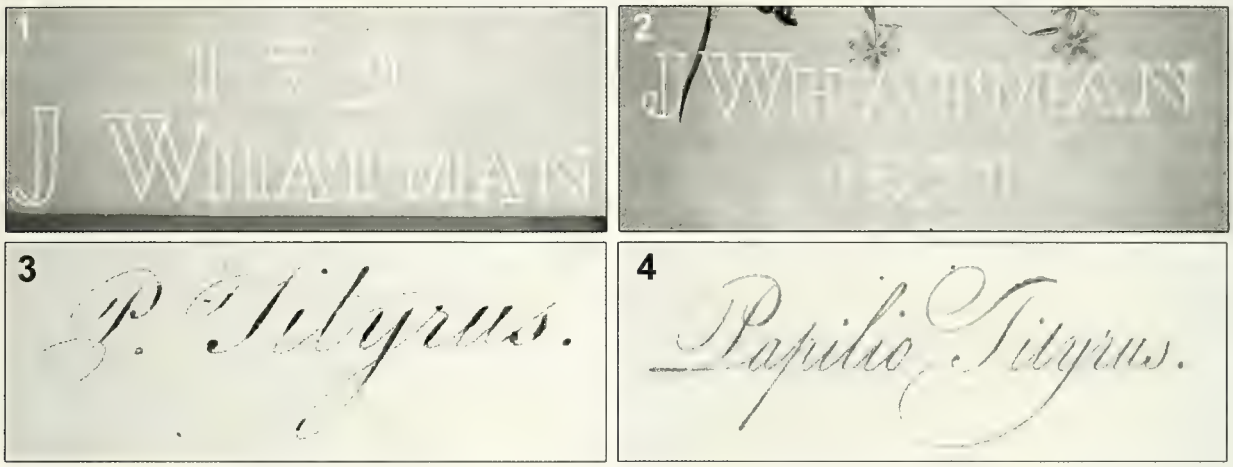
Watermarks. The letterpress and plates of *Insects of Georgia* were printed on fine wove paper from England. Wove paper was invented during the first half of the eighteenth century by English papermaker James Whatman. Wove lacked the furrows of traditional laid paper and was attractive to printers, engravers, and artists. By the 1780s, wove had become more common in paper mills in England and elsewhere. Today, 99 percent of paper is made on a wove wire base (Balston 1992, 1998). *Insects of Georgia* was produced almost exclusively on paper that bears variations of "J Whatman" watermarks.

James Whatman operated his paper mill, called Turkey Mill, at Maidstone, Kent. By the time Whatman died in 1759, Turkey Mill had become the largest paper mill in England (Balston 1992, TM 2004). Whatman's son, James Whatman II, later took possession of Turkey Mill. He sold the business in 1794 to Thomas, Robert, and Finch Hollingworth. The Hollingworths partnered with Whatman's former apprentice, William Balston. This partnership was dissolved in 1807, after which the Hollingworths used "J Whatman/Turkey Mill" watermarks, while Balston used "J Whatman" (Balston 1992). The most famous natural history publication to utilize Whatman paper was *The Birds of America* by John J. Audubon (1827–1838). John Abbot rendered some of his illustrations on Whatman paper. Mariamne Johnes also used this paper for her correspondence with Smith. After 260 years, through the legacy of W. Balston, the Whatman name is still associated with the manufacture of paper (Whatman 2004). The surviving buildings of the Turkey Mill complex have been converted into a business park that currently houses over fifty companies (TM 2004).

Watermarks are extremely useful in addressing questions involving suspected reissues of books and engravings. They are sometimes separated into watermarks (names and dates) and countermarks (designs). I followed the traditional classification and considered all these elements to be watermarks. Dated watermarks were rare in British papers prior to 1794 and were not always updated annually until about 1810 (Balston 1992). Nonetheless, watermarks can be valuable in establishing chronology for copies of *Insects of Georgia*.

Wilkinson (1981, 1982) and Rogers-Price (1983) observed that plates in copies of *Insects of Georgia* had watermarks dated well into the 1820s. Heath (1982, 1990, 1999) and Leab (1984, 1998) listed seven copies with later watermarks. Wilkinson (1982) studied 35 sets of the book and found that many exhibited this disparity. Unfortunately, a planned summary of his findings was not published. Rogers-Price (1983) suggested that the book was reissued after 1827, with work beginning on reprinting the plates after 1817.

In an effort to better understand these watermarks, I attempted to locate and examine as many surviving copies of *Insects of Georgia* as possible. I ultimately found 80 copies in six countries. Through the assistance of numerous librarians and owners, watermark information was recorded for each copy (Table 2). Seventy years ago, Georgia naturalist Lucian Harris, Jr. knew of only three "perfect sets of this rare old work being carefully preserved in Georgia" (Harris 1931). Today, no fewer than nine copies reside in the state.



FIGURES 1-4. Dated watermarks and plate captions from *Insects of Georgia*. **1**, "1794/J Whatman" watermark on a letterpress leaf. **2**, Balston "J Whatman/1821" plate watermark. **3**, Handwritten caption, Plate 19, first issue. **4**, Engraved caption, Plate 19, early reissue.

Versions of Whatman watermarks in copies of *Insects of Georgia* are "J Whatman," "1794/J Whatman," "J Whatman/18[--]," "J Whatman/Turkey Mills/1817," and "J Whatman/Turkey Mill/1822" (Figs. 1, 2). Later watermarks are larger; "1794/J Whatman" measure 13 cm × 3.8 cm (5 in ×1.5 in), while "J Whatman/Turkey Mills/1817" measure 26 cm × 9.5 cm (10.25 in × 3.75 in). Regardless of the dates on the plates, the letterpress leaves in all copies of *Insects of Georgia* are watermarked "1794/J Whatman" (Figs. 1, 2). Dates found in association with Whatman watermarks on plates are 1794, 1817, 1820, 1821, 1822, 1823, and 1827 (Table 2). Watermarks usually run lengthwise on the sheets and are located at the fore edges of the leaves or in the gutters near the binding. The year associated with Watermarks of "J Whatman/Turkey Mills (with an "s") was frequently truncated or completely cropped when the plates were trimmed and bound. Complete "Turkey Mills" watermarks were found to be associated only with the year 1817, thus such marks with unidentifiable dates were listed as "[1817]" on Table 2. Paper with "Turkey Mill(s)" watermarks originated from the Hollingworth operation at Turkey Mill, Maidstone. Paper with "J Whatman" watermarks dated after 1794 originated from the Balston paper mill at nearby Springfield. Similar variations of Whatman watermarks have been documented on plates in Audubon (1827–1838) (Low 2002, Steiner 2003).

The single plate watermarked "J Whatman/1827" was found in a copy of *Insects of Georgia* deposited in the Hargrett Rare Book and Manuscript Library, University of Georgia (Table 2). This set was originally owned by Franklin College, the forerunner of the University of Georgia. Interestingly, at least seven plates in this copy bear partial watermarks of "& S" and "II". Such watermarks were also found in copies in the John Carter Brown Library (Brown University), John Hay Library (Brown University), Hill Memorial Library (Louisiana State University), Morris Museum of Art, and the New York Public Library. Plates in these copies are watermarked 1820–1822 (Table 2). All watermarks of "& S," "S," and "II" were found in association with the year 1820. I was unable to identify this papermaker. Even a contact at the British Association of Paper Historians was unfamiliar with these watermarks. These copies of the book may have been among the last assembled, utilizing less expensive paper to complete the plates for these volumes. Flyleaves in a reissue copy in the Library of Congress (Table 2) bear watermarks of "W. Venables/1824." These blank pages were most likely added by the bookbinder. Other surviving reissues probably also contain a mixture of papers, but consist mainly of Balston and Hollingworth product (as "J Whatman"). American lepidopterist William J. Holland may have been aware of later watermarks, including the 1817 dates in his own personal copy now in the Carnegie Museum of Natural History. In Holland (1898), he did not say that the book was published in 1797, but rather that it "appeared in two folio volumes, bearing the date of 1797."

Plate captions. Dunthorne (1938) observed that plates of *Insects of Georgia* were irregularly produced without numbers and names. I compared plate captions in 23 copies of the book (Table 3) and discovered that their presence and position is variable, particularly in copies with watermarks dated later than 1794. These elements are engraved on some plates and handwritten on others. Many lack plate captions entirely.

TABLE 2. Dated plate watermarks in copies of Insects of Georgia. State of plates 77 & 78: 1 = uncorrected; 2 = corrected.

Repository	No. copies	Dates recorded	States of plates 77 & 78
1. American Museum of Natural History Research Library (New York, New York)	1	1820, 1821, 1822	
2. Atlanta History Center (Atlanta, Georgia)	1	1794, 1820, 1821, 1822	77: 1, 78: 1
3. Bancroft Library, University of California, Berkeley (Berkeley, California)	1	1794	
4. Beinecke Rare Book and Manuscript Library, Yale University (New Haven, Connecticut)	1	[1817], 1822	7: 1, 78: 1
5. Bibliothèque Nationale de France [National Library of France] (Paris, France)	1	1794	
6. Bio-medical Library, University of Minnesota (Minneapolis, Minnesota)	1	1794	
7. Birmingham Public Library (Birmingham, Alabama)	1	1794	
8. Bodleian Library, Oxford University (Oxford, England)	1	1794	77: 2, 78: 2
9. British Library (London, England)	3	1794 (all copies)	77: 2, 78: 2 (all copies)
10. Buffalo & Erie County Public Library (Buffalo, New York)	1	1817	
11. Canadian Agriculture Library (Ottawa, Ontario, Canada)	1	none found	
12. Carl A. Kroch Library, Cornell University (Ithaca, New York)	1	1794	
13. Carnegie Museum of Natural History Library (Pittsburgh, Pennsylvania)	1	1817	77: 1, 78: 1
14. Charleston Library Society (Charleston, South Carolina)	1	1794	
15. Doheny Memorial Library, University of Southern California (Los Angeles, California)	2	copy 1: 1794 copy 2: [1817], 1821, 1822	
16. Ellis Library, University of Missouri-Columbia (Columbia, Missouri)	1	1822	77: 1, 78: 2
17. Entomology Library, The Natural History Museum, London England)	2	copy 1: 1794 copy 2: 1821, 1822	77: 2, 78: 2 77: 1, 78: 1
18. Ernst Mayr Library of the Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts)	1	1794, 1817	77: 1, 78: 1
19. Ewell Sale Stewart Library, The Academy of Natural Sciences of Philadelphia (Philadelphia, Pennsylvania)		1794, 1817	77: 1, 78: 1
20. Fitzwilliam Museum (Cambridge, England)	1	1794	77: 2, 78: 2
21. Hamilton Library, University of Hawai'i (Manoa, Hawai'i)	1	1794	77: 2, 78: 1
22. Hargrett Rare Book and Manuscript Library, University of Georgia (Athens, Georgia)	4	copy 1: 1794, 1820, 1821, 1822, 1827 copy 2: 1794, 1817, 1821, 1822, 1823 copy 3: 1794 copy 4: none (vellum) plate guards 1801	77: 1, 78: 2 77: 2, 78: 1 77: 2, 78: 2 77: 2, 78: 2
23. Hill Memorial Library, Louisiana State University (Baton Rouge, Louisiana)	1	1794, 1820, 1821, 1822	77: 1, 78: 2
24. Hope Library of Entomology, Oxford University (Oxford, England)	1	1794	77: 2, 78: 2
25. Houghton Library, Harvard University (Cambridge, Massachusetts)	1	1794	

TABLE 2. (continued) Dated plate watermarks in copies of Insects of Georgia. State of plates 77 & 78: 1 = uncorrected; 2 = corrected.

Repository	No. copies	Dates recorded	States of plates 77 & 78
26. Howard-Tilton Memorial Library, Tulane University (New Orleans, Louisiana)	1	1794	
27. Ina Dillard Russell Library, Georgia College & State University (Milledgeville, Georgia)	1	1794	
28. John Carter Brown Library, Brown University (Providence, Rhode Island)	1	1820, 1821,1822	
29. John Crerar Library, University of Chicago (Chicago, Illinois)	1	1820, 1822	77: 1, 78: 2
30. John Hay Library, Brown University (Providence, Rhode Island)	1	1820, 1821, 1822	
31. John Hinchliff, personal library of Florence Hinchliff (Portland, Oregon)	1	none found	
32. John M. Olin Library, Washington University (St. Louis, Missouri)	1	1794	
33. John Rylands University Library of Manchester (Manchester, England)	1	1794	
34. John V. Calhoun, personal library (Palm Harbor, Florida)	1	1794, [1817], 1821, 1822	77: 1, 78: 1
35. Joseph F. Cullman 3rd Library of Natural History, Smithsonian Institution	1	1794	77: 2, 78: 2
36. Library and Archives Canada (Ottawa, Ontario, Canada)	1	1794, 1820, 1821, 1822	
37. Library of Congress (Washington, D.C.)	1	1794, 1821, 1822, 18[23]	77: 2, 78: 1
38. Linnean Society of London (London, England)	1	1794	77: 2, 78: 2
39. Lucy Lester Willet Memorial Library, Wesleyan College (Macon, Georgia)	1	1794, [1817], 1821, 1822	
40. The LuEsther T. Mertz Library, The New York Botanical Garden (New York, New York)	1	none found	77: 1, 78: 1
41. Macdonald Campus Library, McGill University (Montreal, Quebec, Canada)	1	1794	77: 2, 78: 1
42. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Univ of Florida, (Gainesville, Florida)	1	1794	77: 2, 78: 2
43. Memorial Library, University of Wisconsin (Madison, Wisconsin)	1	1821, 1822, 1823 (flyleaves 1824)	77: 1, 78: 1
44. Michigan State University Library (East Lansing, Michigan)	1	1794	77: 2, 78: 2
45. Missouri Botanical Garden Library (St. Louis, Missouri)	1	1794	77: 2, 78: 2
46. Morris Museum of Art (Augusta, Georgia)	1	1820, 1821, 1822	77: 2, 78: 2
47. National Agriculture Library (Beltsville, Maryland)	1	[1817]	77: 1, 78: 1
48. New York Public Library (New York, New York)	1	1820, 1821, 1822	
49. Niedersächsische Staats- und Universitätsbibliothek Göttingen [Göttingen State and University Library] (Göttingen, Germany)	1	1794	
50. Olin Memorial Library, Wesleyan University (Middletown, Connecticut)	1	1794	77: 2, 78: 2
51. Österreichische Nationalbibliothek [Austrian National Library] (Vienna, Austria)	1	1794	
52. Parks Library, Iowa State University (Ames, Iowa)	1	1794	77: 2, 78: 2

TABLE 2. (continued) Dated plate watermarks in copies of Insects of Georgia. State of plates 77 & 78: 1 = uncorrected; 2 = corrected.

Repository	No. copies	Dates recorded	States of plates 77 & 78
53. Pennsylvania Hospital Medical Library (Philadelphia, Pennsylvania)	1	1794	77: 2, 78: 1
54. Public Library of Cincinnati and Hamilton County (Cincinnati, Ohio)	1	1822	77: 1, 78: 2
55. Radcliffe Science Library, Oxford University (Oxford, England)	1	1794	77: 2, 78: 2
56. Rare Book, Manuscript and Special Collections Library, Duke University (Durham, North Carolina)	1	[1817], 1821, 1822	77: 2, 78: 1
57. Royal Entomological Society Library (London, England)	1	1794	77: 2, 78: 2
58. Sächsische Landesbibliothek-Staats- und Universitätsbibliothek Dresden [Saxon State Library and University Library] (Dresden, Germany)	1	1794	
59. South Caroliniana Library, University of South Carolina (Columbia, South Carolina)	1	1817	77: 1, 78: 1
60. Sutro Library, California State Library (San Francisco, California)	1	[1817]	77: 1, 77: 1
61. Tampa-Hillsborough County Public Library (Tampa, Florida)	1	1817	77: 1, 77: 1
62. Thomas Cooper Library, University of South Carolina (Columbia, South Carolina)	1	1794	77: 2, 78: 2
63. Thomas J. Dodd Research Center, University of Connecticut (Storrs, Connecticut)	1	1794	77: 2, 78: 2
64. Thomas Rare Book Library, Wittenberg University (Springfield, Ohio)	1	1794	77: 2, 78: 2
65. Tracy W. McGregor Library, University of Virginia (Charlottesville, Virginia)	1	1817	
65. University College of London (London, England)	1	1794	77: 2, 78: 1
66. University Library, University of Cambridge (Cambridge, England)	2	copy 1: none found copy 2: 1794, [1817]	77: 2, 78: 2 77: 1, 78: 1
67. University of Illinois Library (Urbana-Champaign, Illinois)	1	1794, 1820, 1821, 1822, 1823	77: 1, 78: 1
68. W. E. B. Du Bois Library, University of Massachusetts (Amherst, Massachusetts)	1	1817	77: 1, 78: 1
69. Warren N. Baggett, printseller (Franklin, Tennessee) (plates sold 2003–2004)	1	1817	
70. Wilson Library, University of North Carolina (Chapel Hill, North Carolina)	1	1794	77: 2, 78: 2
71. Woodruff Library, Emory University (Atlanta, Georgia)	1	1822, 1823	
Book auction records	1		
1. 20 November 1981 (Heath 1982, Leab 1984)	1	1821, 1822	
2. 8 December 1989 (Heath 1990)	1	1820, 1822	
3. 14 June 1990 (Heath 1990)	1	1794, 1820, 1821, 1822	
4. 15 June 1990 (Heath 1990)	1	1820, 1822, 1823	
5. 1993 (McGrath 1993)	1	1794	
6. 3 June 1997 (Leab 1998, Heath 1999)	1	1817	
7. 13 June 2002 (Christie's 2002)	1	"later issue" (dates unknown)	
8. 19 November 2003 (Christie's 2003)	1	"later issue of around 1822"	

TABLE 3. Captions on plates in copies of *Insects of Georgia*. Copies marked by an asterisk (°) were personally examined (digital photos for copy 18). Plates that lack captions are not listed.

Copy examined	Watermarks	Handwritten ink captions	Engraved captions
1. Bodleian Library, Oxford University (Oxford, England)	1794	none	1-104
2. Charleston Library Society (Charleston, South Carolina)	1794	1-3, 5, 7-54, 56-104 (Plate 4 missing)	6
3. Entomology Library, The Natural History Museum, London (London, England) (copy 1)°	1794	1-104	none
4. Entomology Library, The Natural History Museum, London (London, England) (copy 2)°	[1817], 1821, 1822	42, 57, 77	2, 3, 5, 7, 9, 11, 13, 16, 17, 20-22, 24, 31, 33, 36, 38, 51, 54, 56, 58, 60, 66, 68, 70, 72-76, 84-87, 89, 90, 93-104
5. Ewell Sale Stewart Library, The Academy of Natural Sciences of Philadelphia (Philadelphia, Pennsylvania)°	1794, 1817	10, 40, 42, 57, 77, 82, 91, 97, 104	5, 7, 9, 11-16, 18-21, 26-32, 34, 35, 37, 39, 41, 43, 44, 47-50, 52-55, 58-61, 63-65, 67, 69, 71-74, 76, 79-81, 83, 85-87, 90, 92, 94-96, 98-100, 103
6. Hargrett Rare Book and Manuscript Library, University of Georgia (Athens, Georgia) (copy 1)°	1794, 1820, 1821, 1827	none	1-6, 8-11, 13, 14, 16-19, 21, 22, 24, 25, 27-34, 36-38, 41, 42, 44-46, 49-52, 54-60, 63-77, 79, 80, 83-104 (Plates 7, 48 missing)
7. Hargrett Rare Book and Manuscript Library, University of Georgia (Athens, Georgia) (copy 2)°	1794, 1817, 1821, 1822, 1823	none	2, 3, 5, 7, 8, 10, 11, 13, 16-18, 20-22, 24, 25, 27-33, 35, 38-40, 50-60, 67, 69, 70, 72-74, 76, 77, 79, 81-90, 93-104
8. Hargrett Rare Book and Manuscript Library, University of Georgia (Athens, Georgia) (copy 3)°	1794	58, 78	1-5, 7, 9-57, 59-77, 79-83, 85-104
9. Hargrett Rare Book and Manuscript Library, University of Georgia (Athens, Georgia) (copy 4)°	none; vellum (plate guards 1801)	None	1-104
10. Hill Memorial Library, Louisiana State University (Baton Rouge, Louisiana)	1794, 1820, 1821, 1822	None	2-8, 10, 11, 13, 14, 16-24, 28-30, 33, 35-38, 41, 42, 44, 46-56, 58-60, 63-74, 76, 78-98, 100-104
11. Howard-Tilton Memorial Library, Tulane University (New Orleans, Louisiana)°	1794	1-104	none
12. Ina Dillard Russell Library, Georgia College & State University (Milledgeville, Georgia)	1794	1-104	none
13. John V. Calhoun, personal library (Palm Harbor, Florida)°	1794, [1817], 1821, 1822	10, 15, 42, 54, 77	2, 3, 5, 7, 11, 16, 17, 20-22, 24, 31, 33, 36, 38, 51, 54, 56, 58, 60, 62, 66, 68, 70, 72-74, 76, 84-87, 89, 90, 93-104
14. Joseph F. Cullman 3rd Library of Natural History, Smithsonian Institution (Washington, D. C.)°	1794	1-104	none
15. Library of Congress (Washington, D. C.)°	1794, 1821, 1822, 18[23]	None	2-7, 10, 11, 13, 14, 16-18, 20-22, 24, 25, 27-33, 36, 36, 38, 39, 42, 44, 46, 47, 50-60, 66, 67, 69, 70, 72-74, 76, 77, 79, 82-90, 92-104
16. Linnean Society of London (London, England)°	1794	79	1-7, 9-78, 80-104
17. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida (Gainesville, Florida)°	1794	None	1-104
18. Missouri Botanical Garden Library (St. Louis, Missouri)°	1794	None	1-104
19. Royal Entomological Society Library (London, England)	1794	72	1-71, 73-104
20. South Caroliniana Library, University of South Carolina (Columbia, South Carolina)°	1817	None	1-27, 29-32, 34, 35, 37, 39, 41-46, 48-50, 52-55, 57-61, 63-65, 67, 69-74, 76, 80-104
21. Tampa-Hillsborough County Public Library (Tampa, Florida)°	1817	77	1-4, 6-32, 34, 35, 37, 41-50, 52-55, 57-61, 63, 65, 67, 70-74, 76, 80-90, 92-104
22. Thomas Cooper Library, University of South Carolina (Columbia, South Carolina)°	1794	10, 33	1-9, 11-32, 34-104
23. Thomas Rare Book Library, Wittenberg University (Springfield, Ohio)	1794	None	1-104

Plates in copies 1–3, 8, 11, 12, 14, 16–19, 22, and 23 (Table 3) are watermarked 1794. The plates in copies 3, 11, 12, and 14 have handwritten numbers at the head (top) of the sheets and handwritten Latin insect names centered at the foot (bottom). These captions were inscribed in black ink by at least two calligraphers and the Latin genus names are almost always abbreviated (Fig. 3). Only in rare instances is the genus written out completely. The names were drafted in pencil with horizontal guidelines and overwritten in ink, after which the guidelines were erased. This process is clearly demonstrated by the unfinished name on Plate 70 in copy 13, which is written in pencil and still includes guidelines. Faint traces of guidelines are also present on plates in other copies of the book. All such plates bear watermarks of "1794/J Whatman" or undated watermarks of "J Whatman" suggestive of paper manufactured prior to 1794. The etched signature of John Harris is rarely present at the foot of plates that have handwritten captions.

The plates in copies 1, 17, 18, and 23 have engraved captions (Fig. 4). Copy 18 is currently available for viewing on the Internet (MBG 1995–2005). The captions on the vellum plates at the University of Georgia (copy 9) are also engraved. Engraved captions include a small number at the head of the sheet, a full Latin insect name at the left foot, and a full Latin plant name at the right foot. Plate 68 lacks a plant name in all copies because the plant was not identified in the corresponding letterpress. Engraved captions are identical between the same plates in different copies of the book, regardless of watermarked dates. At least two letter engravers were responsible for adding these elements to the copper plates. The etched signature of John Harris is present at the foot of many more of these plates than those with handwritten captions or none at all. A memorandum about the book by J. E. Smith, dated 19 February 1798, is inserted into copy 1 (see below). The captions in this copy are engraved, thus captions were evidently added to the copper plates prior to February 1798.

Copies 8, 16, 19, and 22 are primarily comprised of plates with engraved captions, but they also contain several plates with captions that are handwritten and/or lacking. Copy 16 was assembled within ten years after 1797, as it was presented to the Linnean Society between 1805 and 1807 (Anonymous 1807a). Copy 20 was listed in an 1807 catalog of books belonging to the South-Carolina College (now Univ. of South Carolina) (Anonymous 1807b) and was likewise produced within ten years after the first printing. Copy 2 is just the opposite, with only one plate bearing engraved captions. Captions were engraved at the wrong end of the copper plate for Plate 30, resulting in an inverted image when the finished prints were bound (it is correctly oriented on plates with handwritten captions). The captions on Plate 53 were also engraved incorrectly, but this can probably be attributed to Smith who wrote notations on the wrong end of the original drawing.

Plates in copies 4–7, 10, 13, 15, 20, and 21 (Table 3) are watermarked with a variety of dates. These plates are much more irregular, with captions that are engraved, handwritten, or lacking entirely. Caption variability is greatest in copies watermarked later than 1817. Copies 4 and 13 are extraordinarily similar and were probably assembled at the same time; the mixture of plates, board decorations, and yellow marbled endpapers are comparable.

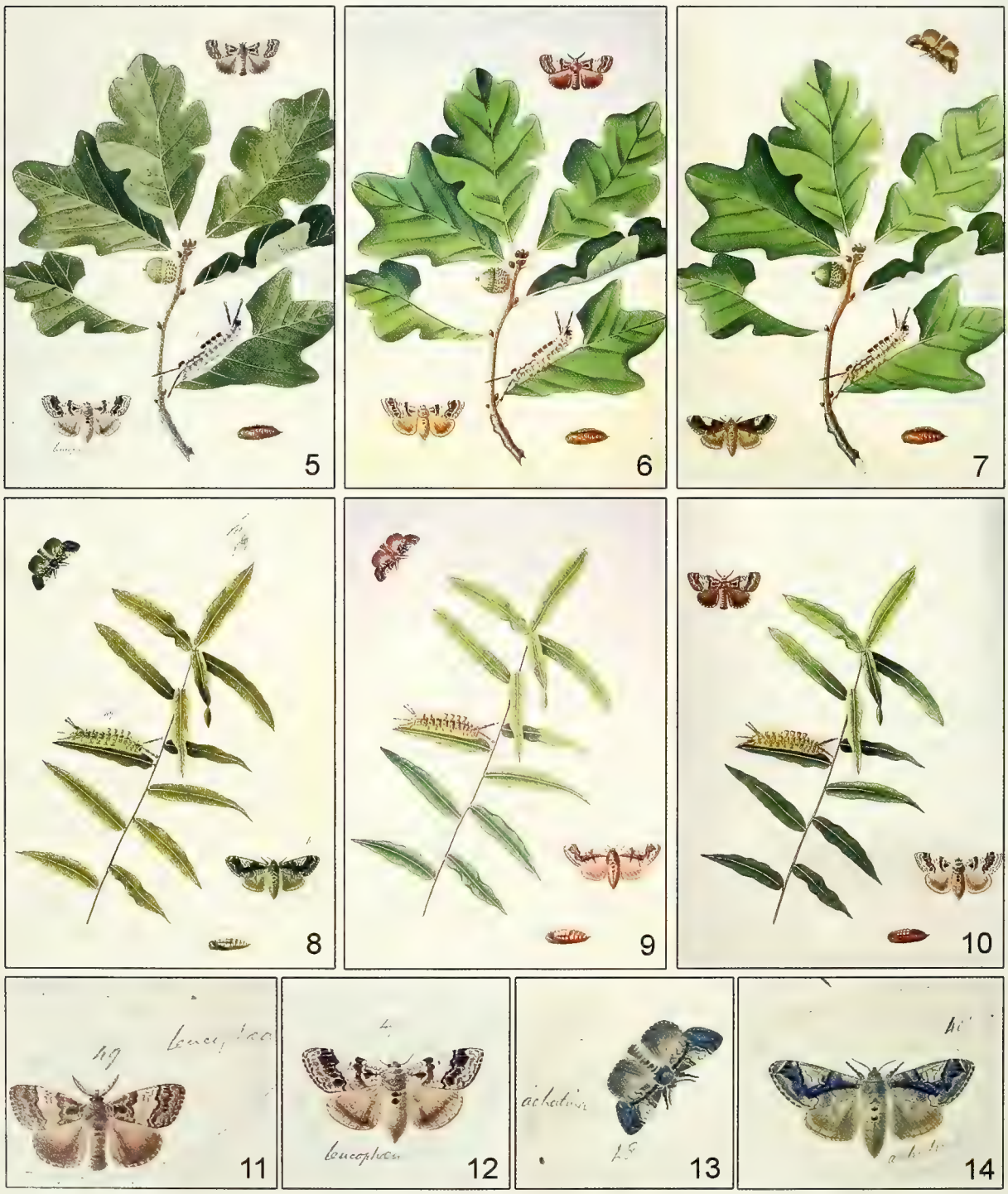
The *Dasychira* discrepancy. The letterpress for Plate 77 in *Insects of Georgia* described *Phalaena achatina* J. E. Smith, treated by Ferguson (1978) as a synonym of *Dasychira meridionalis* (Barnes & McDunnough). However, the adult figures on the accompanying plate are more consistent with *Dasychira basiflava* (Packard). Ferguson (1978) also observed that these figures resembled D. *basiflava*, but he was unaware of valid records of the species from Georgia where it is now known to occur. Although described earlier than *D. basiflava*, *P. achatina* is a junior homonym and not an available name for this species (Ferguson 1978).

The letterpress for Plate 78 described *Phalaena leucophaea* J. E. Smith, now recognized as *Dasychira leucophaea*. The figured female is consistent with *D. leucophaea*, but the male more closely resembles *Dasychira manto* (Strecker). Abbot's association of two different species is understandable, given that *D. manto* was not recognized until 1900. Fortunately, Ferguson (1978) designated the female specimen figured on Plate 78 as the lectotype of *P. leucophaea*.

After consulting a copy of *Insects of Georgia*, Thaddeus W. Harris identified a species of moth as "the *leucophaea*...figured in Mr. Abbot's sumptuous work on insects of Georgia" (Harris 1841). However, Harris' descriptions of the adults and early stages are not consistent with the figures of *P. leucophaea*, but rather those of Smith's *P. achatina*. Harris had reversed the identity of these moths. Over a century later, Ferguson (1978) noted that Plates 77 and 78 appeared to be reversed in a copy of *Insects of Georgia* that he consulted in the Beinecke Library, Yale University. Rogers-Price (1983) also observed this discrepancy in various copies. My analysis of these plates showed them to conform to the adjacent letterpress in most copies of the book that bear only 1794 watermarks. However, the majority of copies with later watermarks appeared to

have these plates reversed. A closer inspection revealed that the plates themselves were not reversed, only the figures of the adult moths (Figs. 6, 7, 9, 10).

For insight into these alterations, I consulted Abbot's original drawings. The adult figures in both drawings are circled and named in pencil in Smith's hand (Figs.



FIGS. 5-14. Original drawings and plates of *Dasychira* from *Insects of Georgia*. **5**, Original drawing for Plate 77°. **6**, Uncorrected Plate 77. **7**, Corrected Plate 77. **8**, Original drawing for Plate 78°. **9**, Uncorrected Plate 78. **10**, Corrected Plate 78. **11**, Original male of *P. leucophaea* (*D. manto*?) (annotations by J. E. Smith)°. **12**, Original female of *P. leucophaea*°. **13**, Original male of *P. achatina* (*D. basiflava*)°. **14**, Original female of *P. achatina* (*D. basiflava*)°. (°The John Work Garrett Library of the Johns Hopkins University).

11–14). The adults on the drawing used for Plate 77 are identified as "*leucophaea*" and those on the drawing for Plate 78 are identified as "*achatina*." On the drawing for Plate 77, Smith also labeled the plant and early stages as "48" and the adult moths as "49." He wrote just the opposite on the drawing for Plate 78.

Abbot's manuscript at the Linnean Society holds the key to understanding Smith's mysterious notations and plate alterations. The numbers "48" and "49" correspond to Abbot's entries for these drawings. Under entry no. 49 (page 22) Abbot wrote, "These is misplaced by mistake, too late to remedy it in the Drawing. That is the Worm & Chrysalis, & Description of No. 48 ought to be put to the Moths No. 49. And the

TABLE 4. "Corrections & Emendations" for Insects of Georgia by J. E. Smith, 1798 (Bodleian Library, Oxford University).

Plate no.	Depicted insect species	Comments by Smith
11	*Polygonia interrogationis* (Fabricius)	*Tab. 11. This, I am now convinced, is a distinct species from the true Papilio C aureum of Linnaeus, and may be called Papilio C fractum. P. N. alis dentatis caudatis fulvis nigro maculatis: posticis subtus C argenteo diffracto notatis. P. C aureum Fab. Ent. emend. V. 4. 78.*
NOTES: Smith was correct, but he failed to publish his new name. Fabricius published his description of *Papilio interrogationis* that same year. Smith's Latin narrative is a modified version of Fabricius' description of *C. aureum* with added emphasis on the two-part silvery spot ("argenteo diffracto notalis") on the ventral hindwing. Harris (1841) compared this spot to a semicolon, but Fabricius' name implies a question mark (hence the species' current English name, "Question Mark"). "P. N." refers to the Linnaean classification categories of "Papilio" and "Nymphales."		
13	*Neonympha areolatus* (J. E. Smith)	*Tab. 13. Papilio areolatus, Is supposed by some very intelligent critic, who reviewed this work in the Analytical Review for Jany. 1798, to be Pap. Canthus Linn. Syst. Nat. 768. Fab. Ent. emend. V. 4. 157, of which there is no specimen in the Linnaean cabinet, so that I cannot determine the point.*
NOTES: The reviewer wrote, "of the thirteenth plate...we cannot help recognizing the *canthus* of Linné and Fabricius...The more detailed description of Fabricius confirms the identity of the insect in question" (Anonymous 1798). Smith, however, was correct to describe this as a new species. *Papilio canthus* Linnaeus is a junior synonym of *Satyrodes eurydice* (L.).		
15	*Celastrina neglecta* (W. H. Edwards)	*Tab. 15. Papilio Argiolus. Mr. Jones rather believes this a new species, distinct from the Argiolus of Linnaeus.*
NOTES: Smith was referring to a letter he received from William Jones dated 9 Sept. 1797 (Linnean Society of London), in which Jones argued, "You are certainly wrong in naming the fly *Argiolus* Tab. 15. I have both male and female among my drawings without a name. *Argiolus* is certainly different."		
32	*Agrius cingulatus* (Fabricius)	*Tab. 32. Sphinx Convolvuli. The abovementioned writer in the Analytical Review thinks the insect in this plate the S. cingulata Fab. V. 4. 375, with whose description indeed it admirably accords. If so, Fabricius should have quoted Drury V. 1. t. 25. f. 4 under his cingulata, & not under Convolvuli. I still however think it scarcely more than a variety of the latter.*
NOTES: The reviewer was correct, asserting, "in our eyes it appears to answer in every respect to the *cingulata* of Fabricius" (Anonymous 1798). *Agrius convolvuli* (Linnaeus) is an Old World species that does not occur in North America. As noted by Smith, the figure in Drury (1770-1782) represents *A. cingulatus*, not *A. convolvuli*.		
33	*Manduca sexta* (Linnaeus)	*Tab. 33. Sphinx Carolina. The same writer observes that this species ought to be defined abdomine ocellis quinque parium fulvis, not sex parium. There are however in some specimens rudiments of a sixth pair.*
NOTES: The reviewer firmly stated, "It is surely time to expunge the six yellow pairs of spots that still continue to figure away on the abdomen of this sphinx in the systems, and to substitute five" (Anonymous 1798). Smith's interpretation was more accurate. *Sphinx carolina* Linnaeus is a junior synonym of *Manduca sexta*, whose name refers to the usual presence of six ("sex") pair of fulvous abdominal spots. The reviewer likely confused this species with the similar *Manduca quinquemaculata* (Haworth), which usually has five ("quinque") pair of abdominal spots, but was not described until 1803.		
34	*Manduca rustica* (Fabricius)	*Tab. 34. Sphinx Chionanthi. He remarks also that this insect cannot be the same with Merian's Tab. 5, which, considering the description of the larva, & the account given of the devastation it makes in fields of Cassava, must be taken for the rustica of Fabricius. The name Chionanthi will therefore remain with ours, as a species hitherto nondescript. I had not Merian at hand when I described it.*
NOTES: It was the reviewer's opinion that "with respect to *rustica*...it is clear, that the insect represented by Merian on tab. V, and referred to by Fabricius, in his Ent. Emend. iv, 366, cannot be the same with the sph. *chionanti* [sic]" (Anonymous 1798). These taxa are now considered to be synonymous. The adult moth on Plate 5 in Merian (1705) does appear to be *M. rustica*.		
91	*Catocala vidua* (J. E. Smith)	*Tab. 91. Phalaena Vidua. The reviewer supposes this Noctua Epione of Fabricius, but I think it scarcely accords with his description or Cramer's figure.*
NOTES: The reviewer briefly remarked, "*vidua*, or what we should call *epiope* [sic]" (Anonymous 1798). *Catocala vidua* and *Catocala epione* (Fabricius) are still recognized as separate species. As Smith observed, the dorsal figure in Cramer (1775-1782, Plate 102, fig. E) is most consistent with *C. epione*.		

Worm Chrysalis & Description of this No. 49th to No. 48." Abbot believed that he had mistakenly transposed the early stages of these species.

Abbot did not suggest that the hostplants were reversed in his drawings for these plates. In fact, he seems to have correctly associated the plants with the adult moths. The hostplant in the drawing for Plate 77 is a species of oak, possibly *Quercus stellata* Wangenh. (Fagaceae). The female moth in this drawing, *D. leucophaea*, is an oak-feeder. The male, if *D. manto*, feeds on pine (Pinaceae) (Ferguson 1978). The drawing for Plate 78 depicts a species of Willow, most likely *Salix nigra* Marshall (Salicaceae). The moths in the drawing seem to be *D. basiflava*, which will feed on willow (Ferguson 1978). It would have been far easier, cheaper, and more accurate had Smith left the copper plates as originally etched and simply colored the early stages to resemble the opposite species.

I investigated Plates 77 and 78 in 52 copies of the book (Table 2). All 25 copies bearing only 1794 watermarks contain corrected versions of the plates that rectified Abbot's error. Twenty of these copies include both corrected plates. Conversely, just nine of the 24 copies with later watermarks contain a corrected plate and only one includes both. Two copies have no perceptible watermark dates, but one copy includes both corrected plates. The vellum copy at the University of Georgia has corrected plates. All the prints of Plates 77 and 78 that I personally examined bear only 1794 watermarks. Twelve copies examined during this study possess mixed versions of these plates, absentmindedly including two illustrations of the same species. All the copies examined with watermarks of 1817 or later have captions that are handwritten or lacking on Plates 77 and 78.

Despite Abbot's admitted mistake, the copper plates were initially etched to reproduce the drawings as originally rendered. The moth figures were later re-etched on the same copper plates to correct the error. Small imperfections on both versions of the plates show that the remaining figures were unchanged. Corrected plates were struck with and without engraved captions, thus the moths were re-etched before the captions were permanently added. Calligraphers were sometimes so confused about these plates that they incorrectly wrote the opposite names and numbers on early prints that lacked engraved captions.

Although Abbot advised that his notes for these drawings were also mistakenly reversed, this was not corrected for the book. Abbot combined adults with the "proper" immatures in other sets of drawings. The copy of *Insects of Georgia* that Harris (1841) used to identify *D. leucophaea* was obviously a later reissue with uncorrected versions of Plates 77 and 78, thereby misleading him on the identity of *D. leucophaea*.

Corrections & Emendations. A two-page handwritten memorandum by J. E. Smith entitled "Corrections & Emendations" was discovered in the first volume of *Insects of Georgia* in the Bodleian Library, Oxford University. Signed "J E Smith" and dated "Norwich Feb. 19. 1798," it is the only known document of its kind. Smith wrote to his wife from Oxford on 26 April 1798 and mentioned that he was visiting the "Sherardian Library," now part of the Oxford University herbaria (Smith correspondence, Linnean Society of London). He may have presented this copy of the book at that time.

Smith's comments are mostly in response to an anonymous review of *Insects of Georgia* that was published a month earlier (Anonymous 1798). Smith reconsidered some of his identifications in the book and proposed a new Latin name for the butterfly on Plate 11. The memo was written about six months after the book first appeared and offers valuable insight into Smith's perception of seven species. Few British naturalists of the period could have penned such an erudite review of *Insects of Georgia*. The author, whom Smith called "some intelligent critic," was most likely Edward Donovan, who was actively engaged in publishing books on British and foreign insects at that time. Donovan's prose was similarly eloquent and he was prone to extensive footnoting, which is also evident in the review. Donovan was a great admirer of Linnaeus and Fabricius, who were often mentioned in the review, particularly within the footnotes. Moreover, Donovan (1798) discussed *Insects of Georgia* and mentioned the work of Abbot, acknowledging, "our cabinet is indebted to his labours for several hundred species, altogether new in Europe." The remarks of Smith and the reviewer are reproduced in Table 4.

Spine titles and authorship. Surviving copies of *Insects of Georgia* that are thought to possess original bindings vary considerably in how the title and author were printed on the spine. Copies attributed to early issues often exhibit very similar titles, such as "Smith's American Insects," "Abbot's American Insects," "Abbot's and Smith's American Insects," and "Insects of America." The binding on the original drawings given to Mariamne Johnes is consistent with other early copies, reading "Smith's American Insects." The copy with the vellum plates reads "Abbot's American Insects." Spine titles on later copies are more variable, reading "Insects of Georgia," "Lepidopterous Insects," "Lepidopterous Insects of Georgia," "Natural History of Insects," and "Natural History of Lepidopterous Insects." Author designations also vary, with later copies

often citing them separately from the title, as "Abbot," "Smith," or "Smith & Abbot." These differences probably reflect the changing titles on the printer's boards over the many years that the book was issued and bookbinders simply reproduced them as given.

Irregular author attributions are also reflected in the literature, with most crediting Smith & Abbot, Abbot & Smith, or just Smith. In the preface of the book, Smith characterized himself as merely the "Editor," leading Kirby & Spence (1815–1826) to cite the book as "Smith's Abbott's Insects of Georgia." Westwood (1840) could not decide who the senior author was, citing both Smith & Abbot and Abbot & Smith. Duncan (1841) considered Smith to be the junior author who "superintended the arrangement." Since about 1980, the book trades have consistently credited Abbot or Abbot & Smith in sales lists and catalogs. I have followed dos Passos (1958) and Wilkinson (1981) who awarded authorship to Smith (as editor) and Abbot (as artist/observer). The double-t spelling of Abbot's name remains a common error. Some authors, such as Westwood (1840) and Audubon (1838), included both the correct and double-t versions within the same publications. The incorrect spelling is even printed on the spines of some copies of *Insects of Georgia*.

Ownership. Over the years, there have been many distinguished owners of *Insects of Georgia*. Many were British, Irish, or Russian royalty, who ranked among the few that could afford such an expensive luxury. Bookplates in surviving copies reveal the following aristocratic owners (numbers correspond to copies in Table 2): Count Nikolai Petrovich Sheremetev (1751–1809) (27), Richard, VII Viscount Fitzwilliam of Merrion (1745–1816) (20), Valentine Browne, 1st Earl of Kenmare (1754–1812) (26), George John, 2nd Earl Spencer (1758–1834) (33), Walter Francis Montagu-Douglas-Scott, 5th Duke of Buccleuch and Queensberry (1806–1884) (25), William Willoughby Cole, 3rd Earl of Enniskillen (1807–1886) (65), Thomas de Gray, 6th Baron of Walsingham (1843–1919) (46), Count Sergei Dmitrievich Sheremetev (1844–1918) (27), and Lionel Walter Rothschild, 2nd Baron Rothschild of Tring (1868–1937) (17, copy 2). Other notable owners were Georgia philanthropist Wymberley Jones De Renne (1853–1926) (22, copy 3), Harvard zoologist Walter Faxon (1848–1920) (18), Icelandic entrepreneur Hjörtur Thórdarson (1867–1945) (43), and Coca-Cola President Charles Howard Candler (1878–1957) (71). Entomologists, both professional and amateur, who possessed personal copies include William Jones (?–1818) (lost?), Jean B. A. D. de Boisduval (1799–1879) (Guenée 1852; lost?), Thomas B. Wilson (1807–1865) (19), William J. Holland (1848–1932) (13), Ellison A. Smyth, Jr. (1863–1941) (42), William Barnes (1860–1930) (35), Edward O. Essig (1884–1964) (3), Cyril F. dos Passos (1887–1986) (64), Lionel G. Higgins (1891–1985) (31), and John Hinchliff (1915–1999) (31). Thomas de Gray and Lionel W. Rothschild were also accomplished amateur lepidopterists. I am extremely fortunate to have recently obtained my own copy (34), originally owned by the Faculty of Physicians and Surgeons, Glasgow, Scotland. My curiosity about its watermarks prompted this study.

Plate sets. Individual plates from *Insects of Georgia* were evidently offered for sale shortly after production of the book was discontinued. The only known surviving set of such plates was once owned by American lepidopterist Cyril F. dos Passos and is now deposited in the Thomas Rare Book Library, Wittenberg University, Springfield, Ohio. It is comprised of 73 bound plates, including one duplicate. According to a typed and handwritten note pasted onto a flyleaf, dos Passos purchased the set unbound in 1961 from London bookseller Wheldon & Wesley for the paltry sum of $56.00 US. Wheldon & Wesley was undoubtedly responsible for the typed portion of this note, as it includes the UK spelling of "coloured." Handwritten additions and corrections appear to have been added by dos Passos. The note describes the set as "An interesting collection as it represents a second issue, apparently unrecorded. Many of the plates are watermarked between 1820 and 1828." This is the earliest known direct reference to later watermarks on plates of *Insects of Georgia*. It is astounding that comparable watermarks in copies of the book were never mentioned in the literature during the preceding 130 years.

This was the only incomplete set of plates known to Wilkinson (1981, 1982), but a similar set with 37 plates was sold at auction in 1980 (Heath 1981). A single plate from an unidentified source was also figured by Rogers-Price (1983). The Wittenberg set includes Plates 1–14, 16–22, 24–26, 31 (2 ea), 32, 33, 36–38, 40, 42, 44–49, 55, 56, 58, 60–76, 84–87, 89, 90, 94–96, 98, 100–102, and 104. The set sold in 1980 included Plates 1–12, 22, 25, 26, 32–34, 36, 40, 44–47, 49, 55, 60–62, 65, 76, 89, 94, and 101–103 (Heath 1981). Ten plates in the Wittenberg set (nos. 1, 6, 12, 18, 25, 32, 33, 45, 46, 61) bear an inscription across the foot of the sheet that reads, "Sold by R Martin. Book & Printseller. 47. Great Queen Strt: Lincolns Inn Fields" (Fig. 15). Seventeen plates in the auctioned set also possessed this inscription (Heath 1981). Most of the plates in the Wittenberg set, particularly those with Martin's inscriptions, were colored with imprecise hues and decidedly sloppy paint application (Figs. 16, 17). Although the "Sold by R.

Martin" inscriptions resemble engraved imprints, they are handwritten in ink and some still possess penciled guidelines. I recently located an 1819 landscape print and an 1828 map that bear the same "Sold by R. Martin" inscriptions (at the University of Portsmouth and a private printseller in London). Rogers-Price (1983) proposed that Martin was the English painter of landscapes, animals, and figurative subjects listed by Wood (1978). However, "Robson's London Directory" for the years 1825–1826 and 1830–1839 listed a book and print seller by the name of Robert Martin who operated primarily from 47 Great Queen Street, Lincoln's Inn Fields, Holborn, London. The individual listed by Wood (1978) was another Robert Martin (son?) who conducted business from a nearby address in Holborn. He was listed separately from the bookseller in 1825–1826 as a "lithographic printer" and as an "artist, engraver, lithographic, & letterpress & copper plate printer" in the London postal directory for 1841. The bookseller was no longer listed in 1841.

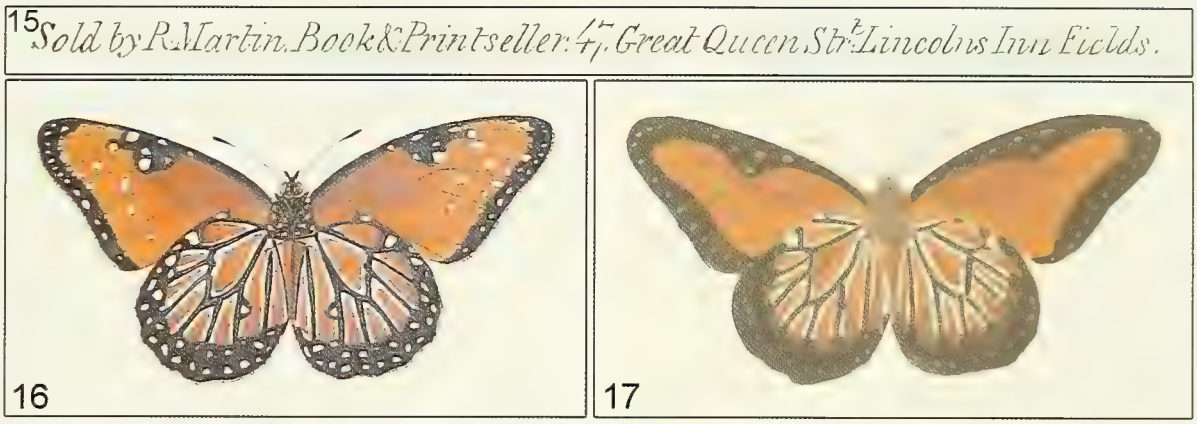
Rogers-Price (1983) supposed that Martin acquired the copper plates, engraved his name, and produced restrikes of the prints for individual sale. However, Martin's inscriptions are handwritten and the plates in the Wittenberg set share characteristics with those contained in later copies of the book. Twelve plates have watermarked dates of 1820, 1821, 1822, and 1828. The plates in the auctioned set were similarly dated 1822–1825 (Heath 1981). The watermarks of the Wittenberg set include "J Whatman/1821" "J Whatman/1822," and "J Whatman/Turkey Mill/1822." Although Wilkinson (1981) attributed all watermarks to Whatman, plates dated 1820 and 1828 are printed on paper with "S" watermarks. Restrikes would all possess engraved captions, but three of these plates lack captions. This evidence refutes the notion that Martin produced restrikes.

Like modern printsellers, Martin probably removed the majority of his prints from broken copies of the book. He also appears to have purchased residual stock of uncolored prints after the last copies of *Insects of Georgia* were assembled. These he colored himself, adding his "Sold by R. Martin" inscription to most of them. The latest watermarked date encountered during this study is 1828, associated with Plate 45 in the Wittenberg set. This plate is badly colored and possesses Martin's "Sold by" inscription, offering additional evidence that Martin obtained residual prints after the book was discontinued. Perhaps due to poor sales, or at the request of customers, Martin combined his remaining inventory into sets of assorted plates. Penciled numbers on many plates in the Wittenberg set may represent Martin's inventory tally.

The true identity of *Papilio bathyllus* J. E. Smith. Original drawings can be instrumental in determining the identity of taxa described and figured in early color plate books (Calhoun 2003, 2004, 2005). Despite their talent, it was difficult for engravers to precisely reproduce every aspect of the original drawings. Some loss of detail was inherent in this process. Moreover, colorists frequently exaggerated or masked pattern elements, further obscuring the identity of figured species and leading to confusion over the status of taxa originally described in these works. To appreciate the phenotypic characters of the species depicted in *Insects of Georgia*, it is important to consult the original drawings. While studying the entomological works of Jacob Hübner, Hemming (1937) also found that "the identity of a specimen figured may be readily resolved if the original drawing is available for study."

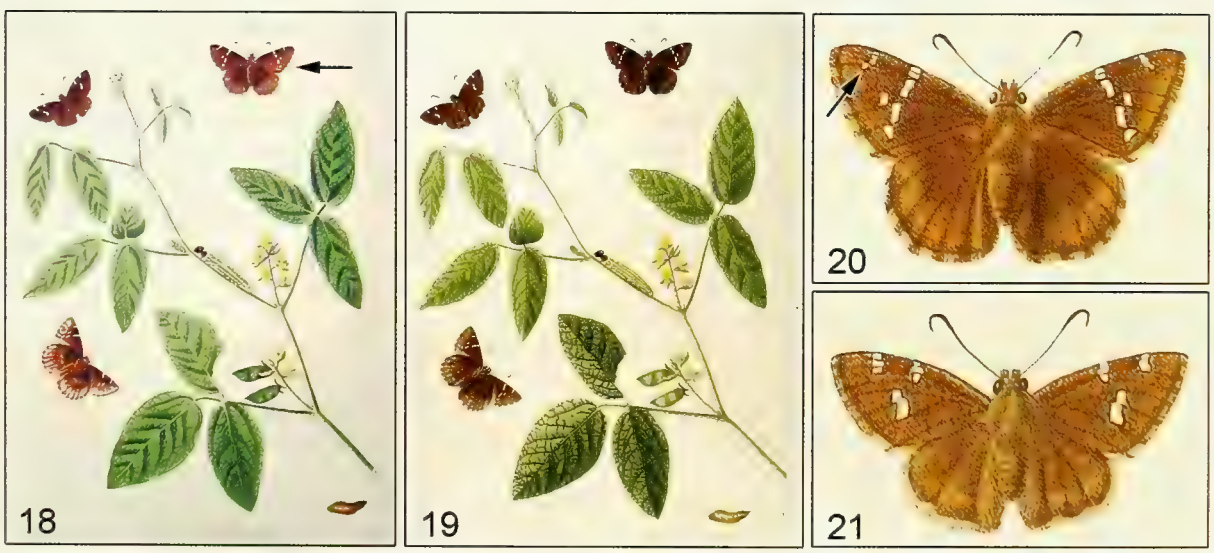
Plate 22 of *Insects of Georgia* portrays a dorsal male, dorsal female, and ventral female that Smith described as *Papilio bathyllus*, now recognized as *Thorybes bathyllus* (Fig. 18). The female figures on the plate possess offset rows of forewing subapical spots. The lowermost spot is distally removed, but is more distinct in some prints than others, depending on the quality of the paint application. In his treatment of *T. bathyllus*, Scudder (1888–1889) referred to rows of spots on the forewings as "three or four closely connected white spots, the lowermost a little smaller than the others and inclined to be removed further toward the tip." Bell (1923) considered these offset subapical spots, the lowest "slightly out of line toward the outer margin," to be a characteristic of his new species, *Thorybes confusis* Bell. Forbes (1960) described these spots on *T. confusis* as tending to "curve out and point up." Gatrelle (2001) concluded that these offset spots are reliable in differentiating *T. confusis* from *T. bathyllus*, which consistently has aligned spots. The male holotype of *T. confusis* in the American Museum of Natural History, as well as five paratypes in the Carnegie Museum of Natural History (figured in Holland 1931, Plate L, figs. 1, 2) and the National Museum of Natural History (USNM), all exhibit offset rows of subapical spots. The female figures on Plate 22 also possess narrow forewing median spots, which is another characteristic of *T. confusis*. I consulted Abbot's original drawing to determine if these pattern elements were intentional or artifacts of the engraving process (Fig. 19). Abbot's original figures possess these features and appear to be most consistent with *T. confusis* (Fig. 20). *Thorybes confusis* is distributed across the southeastern United States and still occurs in eastern Georgia where Abbot presumably collected his specimens (Harris 1972).

The figure of the dorsal female has position



FIGS 15-17. Plate details. **15**, Inscription from R. Martin plate set°. **16**, Ventral male *Danaus gilippus* (Cramer), Plate 7 from a copy of *Insects of Georgia*. **17**, Poorly colored ventral male *D. gilippus*, Plate 7 from the R. Martin plate set°. (°Thomas Library, Wittenberg University).

precedence on both the original drawing and corresponding Plate 22 in *Insects of Georgia* (Figs. 18, 19). Accordingly, it can be argued that the name *Papilio bathyllus* applies to the species now recognized as *T. confusis*. No name-bearing type of *P. bathyllus* exists, but this name has been associated with actual specimens for 207 years, including 82 years after the description of *T. confusis*. The priority replacement of the name *T. confusis* by *P. bathyllus* would result in considerable confusion. To promote nomenclatural stability, I hereby designate Abbot's male specimen, best portrayed in his original drawing (Fig. 21), as the LECTOTYPE of *Papilio bathyllus* J. E. Smith. The forewing pattern of the illustrated figure is somewhat conceptual, but the species is still readily identifiable and easily differentiated from males of *T. confusis*, as well as the third related species in Georgia, *Thorybes pylades* (Scudder). This figure was consulted by Smith for his original description and its etched version has been associated with the name *P. bathyllus* for over two centuries. The specimen that Abbot illustrated probably no longer exists. The type locality of *P. bathyllus* is restricted to Burke County, Georgia, where Abbot lived when he completed this drawing. The lectotype that Ferguson (1978) designated for *Phalaena leucophaea* is likewise better portrayed in Abbot's



FIGS. 18-21. *Thorybes* illustrations. **18**, Plate 22 of *Papilio bathyllus* (arrow indicates dorsal female). **19**, Original drawing for Plate 22°. **20**, Original dorsal female of *P. bathyllus* (*T. confusis*)° (arrow indicates offset subapical spot). **21**, Original dorsal male of *P. bathyllus*°, representing the lectotype. (°The John Work Garrett Library of the Johns Hopkins University).

original drawing, which was unknown to Ferguson. Published figures of these species in *Insects of Georgia* vary from print to print, offering less consistent renditions of Abbot's specimens.

DISCUSSION

Evidence confirms that complete "new" copies of *Insects of Georgia* were assembled for over three decades. Watermarks alone reveal that nearly 50 percent of the copies of *Insects of Georgia* examined during this study were assembled after 1797. Seven of the eight auction records that refer to watermarks also indicate reissues (Table 2). However, dated watermarks cannot be exclusively relied upon to determine issue status. Only four of the 13 copies with 1794 watermarks in Table 3 are thought to be first issues. Based on evidence accumulated during this study, the following is a reasonable account of the production of *Insects of Georgia*.

The first copies were assembled during the summer of 1797. Plates in these copies bear watermarks of 1794 or undated watermarks suggestive of earlier paper. The copper plates were most likely inked with a dabber (dauber), which restricted the ink to the central figures of insects and plants. As a result, the signatures that engraver John Harris etched at the foot of the copper plates did not usually appear on these prints. Many of these prints received handwritten names and numbers. Copies 3, 11, 12, and 14 (Table 3) contain only plates in this format and likely represent first issues. Copy 12 is the only one known to be deposited in Georgia that can be deemed a first issue.

Plates 77 and 78 were struck using the original versions of their copper plates, but the resulting prints were not used for early copies of the book. The moths on these copper plates were re-etched and the resulting new prints were used for initial issues. Captions were engraved on all the copper plates before February 1798, providing consistency and alleviating the need for calligraphers. Unused prints that lacked engraved captions were placed into storage. The presence of engraved captions required that greater portions of the copper plates had to be inked, thereby revealing more of the signatures that Harris etched at the foot of the copper plates. The added cost of employing calligraphers and letter engravers, as well as striking all new plates, probably contributed to the financial loss lamented by publisher James Edwards.

The foreign subject matter of *Insects of Georgia* was not as popular among British and European patrons as Smith's botanical works. As a result, production of the book may have been suspended after 1798. This is suggested by the disposal of the bound original drawings by publisher James Edwards in June 1799. A large amount of letterpress and printed plates remained unused. Probably between 1801 and 1804 a set of prints were stuck on vellum, colored by engraver John Harris, and bound with letterpress into a copy of *Insects of Georgia*. These stunning volumes were possibly created as a device to generate new orders for the book. Alternatively, they were produced as a retirement gift for James Edwards in 1804.

It may have been after the retirement of Edwards that residual letterpress and prints were brought out of storage and additional copies of the book were assembled. Prints with engraved captions were preferred for these copies, but too few remained. To complete these new copies and minimize costs, a few earlier prints without engraved captions were also used. Most of these early prints possessed handwritten captions. Volumes consisting of mixed plates from early impressions were probably produced on an irregular basis for up to twenty years under the pretext of having been assembled in 1797. . By about 1820, early prints with engraved captions were nearly depleted, so new prints were struck on paper dated 1817. More of the early prints without engraved captions were used to complete these new copies. This resulted in a limited issue of books that included plates dated only 1794 and 1817.

Additional copies of the book were assembled ca. 1825–1830. An even greater quantity of early prints without engraved captions was combined with new prints to produce these volumes. Later copies of the book therefore contain an assortment of prints, effectively representing anthologies of preceding impressions. It is unknown if colorists utilized pattern plates to maintain consistency from issue to issue, or if they simply consulted earlier colored prints. Many of the earlier prints may also have been colored just prior to use for later reissues. A large number of copies were assembled during this period, possibly in response to the growing popularity of entomological themes. Ornithologist John J. Audubon was living in London around this time and observed, "Insects, reptiles and fishes are now the rage, and these fly, swim or crawl on pages innumerable in every bookseller's window" (Hart-Davis 2004). The additional steps of printing and coloring plates tripled production costs (Swainson 1840). The use of residual material probably allowed reissues of *Insects of Georgia* to be offered at a lower price. Bohn (1841) listed a probable reissue copy for only £7, 7s.

The letterpress was probably consumed around 1830. Unused plates were sold to Robert Martin and possibly other printsellers who sought to take advantage of the

market interest in zoological prints. Referring to prints or complete copies of the book still available in London during the 1830s, Swainson (1840) observed, "There are many inferior copies on sale among the booksellers, which are offered at a low price, but the original coloured impressions are seldom met with."

Publisher John White retired in 1816, thus it was most likely Cadell & Davies who gained primary control over production of the book after the retirement of J. Edwards in 1804. After the death of Davies, Cadell continued doing business until his own death in 1836. Unfortunately, the fate of the copper plates remains a mystery; they may have been discarded after the death of Cadell. It is unknown how many copies of *Insects of Georgia* were ultimately assembled. There are undoubtedly additional surviving copies of *Insects of Georgia*, while many others have been lost, broken, or destroyed. It is reasonable to conclude that no more than 250 sets were ever produced. Perhaps less than 50 were offered in 1797.

To imply greater value, some modern booksellers have listed copies of *Insects of Georgia* as "first editions". Despite differences on the plates, no edition statement ever appeared and the letterpress was unaltered throughout the life of the book. Five "Errata" on page 214 remained uncorrected. Early publishers routinely offered reissues of books without any indication that they were produced after the initial publication date. All copies of *Insects of Georgia* should be considered as part of the same single edition.

Insects of Georgia remains a revered masterpiece. The accolades of a contemporary reviewer still resonate after two centuries: "We cannot, however, forbear congratulating the dilettante and the student on the pleasure and information they are about to receive from a sedulous perusal and judicious contemplation of such an assemblage of natural curiosities; and we return our thanks to the publisher, equally for the spirit with which he rescued so valuable a collection from obscurity, and the perseverance and taste with which he superintended the execution of the whole" (Anonymous 1798).

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DESCRIPTIONS OF MALES OF TWO SPECIES OF *DICHOMERIS* (LEPIDOPTERA: GELECHIIDAE) SPECIES WITH NEW DISTRIBUTIONAL RECORDS IN MISSISSIPPI AND ALABAMA

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ABSTRACT. The male genitalia of *Dichomeris illusio* Hodges and *D. mimesis* Hodges are described and illustrated. New distribution records for these species are provided.

Additional key words: genitalia, illustration, *Dichomeris illusio*, *Dichomeris mimesis*, Dichomeridinae, Black Belt Prairie

Dichomeris Hübner, one of the largest genera of Gelechiidae in the world, includes 74 species in America north of Mexico (Hodges 1986). The genus includes 58 species that have been recorded from states and provinces east of the Great Plains; of them, 22 species have ranges extending into the Great Plains and the southwestern United States (Hodges 1986). According to Hodges (1986), only 12 species are known from the southwestern United States. During recent years 39 species of *Dichomeris* have been collected in Alabama and Mississippi, and specimens are deposited in the Mississippi Entomological Museum.

Dichomeris is characterized anatomically by the abdominal segment II having a pair of venulae with anterior apodemes not developed, the forewing having CuA_1 and CuA_2 usually stalked, but sometimes connate, male genitalia with a juxta, and female genitalia with a secondary bursa arising from the corpus bursae (Hodges 1986). Based on anatomical variation in these and other characters, Hodges divided the genus into 19 species groups, of which the *setosella* group was the largest with 40 species.

Hosts in 38 plant families have been recorded for more than 100 species of the genus worldwide (Robinson *et al.* 2002). Asteraceae and Fabaceae are the most commonly used hosts. Most of the species feeding on Asteraceae have a Nearctic distribution and belong to the *D. setosella* species group. Most of the species feeding on Fabaceae occur in the Nearctic, Oriental, and Palaearctic Regions. Species of Euphorbiaceae and Sterculiaceae are major hosts of *Dichomeris* in the Oriental Region (Robinson *et al.* 2002).

Hodges (1986) described 40 species of *Dichomeris*, of which seven were known only from females. *Dichomeris illusio* Hodges and *D. mimesis* Hodges were described from two females of each that were collected in Florida and Texas, respectively, and both were included in the *D. setosella* group (Hodges 1986).

The description of the males of *D. illusio* and *D. mimesis* and new distribution records of these species are based on material in the Mississippi Entomological Museum at Mississippi State University. Photographs of the imagos and female genitalia of these species may be found in Hodges (1986) and at the following website: http://www.msstate.edu/org/mississippientmuseum/Researchtaxapages/Gelechiidaehome.html

Dichomeris illusio Hodges

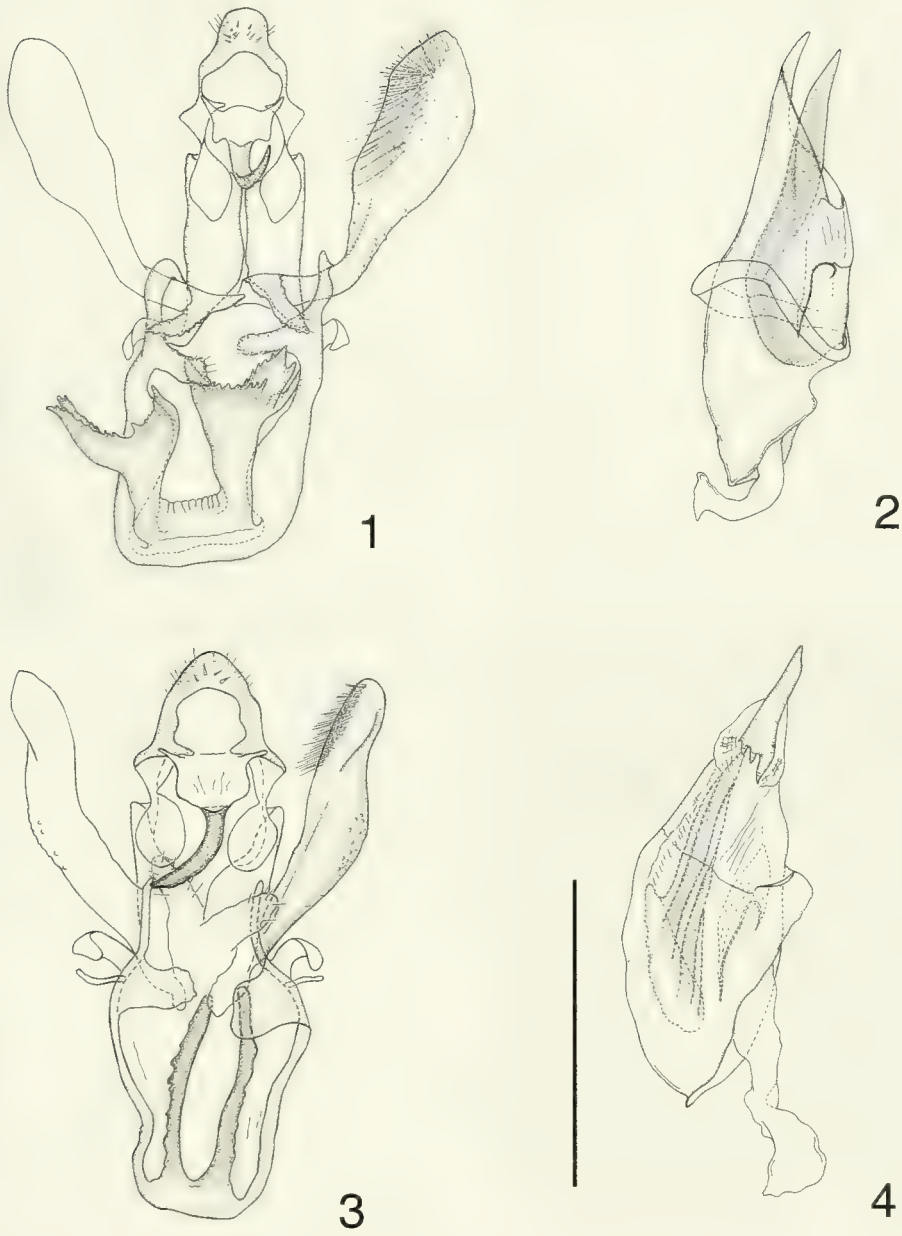
(Figs. 1 and 2)

Thorax: Forewing pattern similar to female; male without scale tuft on anepisternum.

Male genitalia: Valva approximately 1.1× length of tegumen + uncus, abruptly widened near midlength, apical third densely setose on dorsal half; vinculum subequal in length to tegumen + uncus, with a pair of medially projecting lobes arising from near base, lobes sparsely setose apically, saccal region sclerotized and broadly rounded (almost quadrate) ventrally; lobes of juxta arising from common base, broadly bifid, dentate, and sparsely setose apically; aedeagus free from juxta, lateral areas without sclerotized lobes, moderately sclerotized, with more heavily sclerotized plate ventromedially, cornutus broad basally; gnathos with relatively short hook; uncus with apical margin rounded, lateral margins slightly excavated beyond base, dorsal surface with sparse, slender setae, ventral surface with sparse setae, that are stout basally and taper to acute apices.

Material examined: Alabama: Baldwin Co., Bon Secour National Wildlife Refuge, 30°15'09"N 87°48'50"W, 13–15 June 1994, D.M. Pollock (1♂). New state record. Mississippi : Oktibbeha Co., Dorman Lake, 28 June 1984, R.L. Brown (1♂); Winston Co., Noxubee National Wildlife Refuge, T16N R14E Sec 13SE, 14 June 1992, T.L. Schiefer (3♀). New state record.

Notes: Hodges (1986) distinguished *D. illusio* from the superficially similar *D. bolize* Hodges by the distinctive female genitalia. The male genitalia of *D. illusio* differ from those of *D. bolize* and other *Dichomeris* species in having juxtal lobes with bifid and dentate apices. The valvae of *D. illusio* differ from those of *D. bolize* and related species in being abruptly widened near midlength. The characters of the male



FIGS. 1-4. Male genitalia of *Dichomeris* species. Scale bar: 1 mm. 1, *D. illusio*, ventral view, MEM genitalia slide 1005. 2, *D. illusio* aedeagus, lateral view. 3, *D. mimesis*, ventral view, MEM genitalia slide 1006. 4, *D. mimesis* aedeagus, lateral view.

genitalia of *D. illusio* confirm its previous placement by Hodges (1986) in the *D. setosella* group and include the following: vinculum sclerotized in saccal region; aedeagus free, with strong cornutus; uncus well developed, and posterior margin rounded or slightly angled distolaterally.

***Dichomeris mimesis* Hodges**

(Figs. 3 and 4)

Thorax: Forewing pattern similar to female; male without scale tuft on anepisternum.

Male genitalia: Valva approximately 1.1× length of tegumen + uncus, slightly narrowed apically, apical one-fourth of inner surface densely setose; vinculum subequal in length to tegumen + uncus, sinuous ventrally, with a pair of medially projecting, wide lobes arising from near base, lobes moderately setose apically, saccal region sclerotized and slightly rounded; lobes of juxta connected basally on ventral margin of saccus, almost symmetrical, irregularly dentate laterally; aedeagus free from juxta, lateral areas without sclerotized lobes, with more heavily sclerotized plate ventromedially, apex with sclerotized, tapered plate on lateral surface, cornutus broad basally; uncus with apical margin rounded, setae on dorsal surface sparse, slender, setae on ventral surface stout basally, narrowed and tapered near their midlengths.

Material examined: Mississippi: Lowndes Co., T17N R16E Sec 5, 11 March 1991, D.M. Pollock (1♂); Lowndes Co., T17N R16E Sec 34, Black Belt Prairie, 20 May 1992, R.L. Brown (1♂); Oktibbeha Co., T19N R5E Sec 16, 28 May 1990, D.M. Pollock (1♀). New state record.

Notes: All specimens of this species were collected in remnants of the Black Belt Prairie, where several species of insects are disjunct from western states (Brown 2003). The forewing pattern of *D. mimesis* is similar to that of *D. bolize* Hodges, *D. illusio* Hodges, *D. legnotoa* Hodges, and *D. pelta* Hodges. Hodges (1986) stated that "it is possible that the combination of the dark costal margin of the forewing and the shape of the posterior margin of the yellow of the forewing is diagnostic for *mimesis*, but too few specimens are known to be certain." The additional specimens from Mississippi and Alabama have a dark costal margin and two notches on the posterior margin of the yellow band of the forewing, not three as indicated in the key of Hodges (1986); however, this notched margin is much more irregular on the distal half than that in related species as indicated in Hodges' key. The male genitalia of *D. mimesis* differ from superficially similar species by the more narrowly rounded uncus, as compared to the broadly rounded uncus in related species, and by the form of the aedeagus and its sclerotized plate at the apex. The characters of the male genitalia of *D. mimesis* confirm its previous placement in the *setosella* group.

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ECOLOGY AND DISTRIBUTION OF A NEWLY DISCOVERED POPULATION OF THE FEDERALLY THREATENED *EUPROSERPINUS EUTERPE* (SPHINGIDAE)

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ABSTRACT. We discovered a new locality of the federally threatened sphingid *Euproserpinus euterpe* at the Carrizo Plain National Monument in San Luis Obispo County, California. We verified the determination of the species using voucher specimens and diagnostic larval characters. During surveys of the Carrizo Plain, we located the moth along three sandy washes supporting the host plant *Camissonia campestris*, and identified probable individuals at two other sites. The timing of the adult flight was approximately one month earlier than the previously known locality at Walker Basin, spanning late January through February in 2003, but this observation compares different years. Females were observed to oviposit on a pebble and an unpalatable annual plant, which, combined with observed mobility of first instar larvae, leads to the conclusion that oviposition on the exotic weed *Erodium cicutarium* is not maladaptive as has been previously maintained. We hypothesize that natural hydrogeomorphological disturbance is important to maintain habitat features such as young, alluvial sandy soils and dense foodplant along washes. Disturbance from grazing, especially by sheep, appears to harm or destroy habitat, but further research is warranted.

Additional key words: Endangered species, phenology, *Camissonia campestris*, invasive species, *Erodium cicutarium*, grazing, Kern Primrose Sphinx Moth

Euproserpinus euterpe has been listed as threatened under the U.S. Endangered Species Act since 1980 (U.S. Fish and Wildlife Service 1980). The species was originally known as the Euterpe Sphinx (Holland 1903), and later as the Kern Primrose Sphinx Moth (see Osborne 2005). In recent times, it has been known to exist only at one site in the Walker Basin of Kern County, near Bakersfield, California. In 2002, PMJ and Tom Dimock discovered *Euproserpinus euterpe* at two localities within the Carrizo Plain National Monument in San Luis Obispo County, California, over 120 km west of Walker Basin. The discovery of new localities for *Euproserpinus euterpe* provides an unexpected opportunity to secure and manage this threatened species on public land.

Sphingids in the genus *Euproserpinus* are found in arid environments of Alta and Baja California and the Intermountain West. *E. phaeton* is relatively widespread, *E. wiesti* is rare throughout its range across three western states, and *E. euterpe* was thought to be endemic to Kern County in California. The three species are not known to be sympatric at any location (Tuskes and Emmel 1981). Adult *E. euterpe* fly in early spring, with a flight period previously known to range between late February and early April. Longevity of adults is unknown. Females mate soon after eclosion and lay eggs on low-growing forbs and other substrates such as pebbles. Pupation occurs underground, and pupae may remain in diapause for multiple years, a common phenomenon for species of arid landscapes with erratic climates (Powell 1987).

IDENTIFICATION

Euproserpinus euterpe has never before been recorded in the Carrizo Plain, nor indeed anywhere but in the Walker Basin of Kern County (Tuskes and Emmel 1981). Edwards (1888) described the type locality for the species as "San Diego" but this was almost certainly an error (Tuskes and Emmel 1981). The population at Carrizo Plain represents a significant range extension and requires certain proof that the population is *Euproserpinus euterpe*. This requires careful analysis of adult and larval characters.

Two adults from the Carrizo Plain were collected, mounted, and labeled (Fig. 1: Row 1) (currently deposited in the Natural History Museum of Los Angeles County). Moths from the Carrizo Plain share diagnostic characters with those from the Walker Basin (Fig. 1: Row 2), including mixed pale and dark gray scaling on the labial palpus instead of the uniform scales of *E. phaeton* (Hodges 1971). *E. phaeton* shows black scaling of the dorsal surface of the antenna, while

Fig. 1. *Euproserpinus* species, females on left, males on right. Row 1. *Euproserpinus euterpe* - Carrizo Plain population, San Luis Obispo Co., CA. Row 2. *Euproserpinus euterpe* - Walker Basin population, Kern Co., CA. Row 3. *Euproserpinus phaeton* - Mojave Desert population, CA. Row 4. *Euproserpinus phaeton* - Atascadero population, San Luis Obispo Co., CA. Row 5. *Euproserpinus phaeton*, ♂ - Chalone Creek, Pinnacles National Monument, San Benito Co., CA.

scaling is white in *E. euterpe*. White banding on the abdomen is larger and more contrasting in *E. euterpe* than *E. phaeton*. Sensilla chaetica of the antenna are longer in *E. euterpe*. The costal margin of the forewing and hindwing are more convex in *E. euterpe* compared with the flatter and straight margin of *E. phaeton* (K. Osborne, pers. comm.). Based on these adult characters, the two *Euproserpinus euterpe* populations are distinct from the more common *E. phaeton mojave* (Fig. 1: Row 3) found throughout the Mojave Desert and the more coastal *E. phaeton phaeton* (not figured) of Riverside and San Diego counties. A third population of *Euproserpinus* ranges from Atascadero, San Luis Obispo County (Fig. 1: Row 4) at least north to Pinnacles National Monument, San Benito County (Fig. 1: Row 5). Adults of these moths have *E. phaeton* characters, but the larvae exhibit mixed characters: the first instar lacks the black thoracic shield diagnostic of *E. euterpe*, but the fifth instar exhibits typical coloration and pattern of *E. euterpe* from the Carrizo Plain (see below). Pending further analysis, we do not believe that this population is conspecific with *E. euterpe*.

Larvae of the moths at Carrizo Plain exhibit additional diagnostic characters. Tuskes and Emmel (1981) reported that the first instar larva of *Euproserpinus euterpe* is divergent from its congeners, *E. phaeton* and *E. phaeton mojave*. They report that "[t]he thoracic shield, anal horn, and patches on the prolegs are heavily sclerotized and dark brown or black in *euterpe*, but are not sclerotized and green in *phaeton*." First instar larvae from the Carrizo Plain exhibit the *euterpe* character (Fig. 2: Row 1). A second diagnostic character is found in the illustrations of larval forms by C. M. Dammers archived at the Natural History Museum of Los Angeles County. In these illustrations, Dammers depicts the last instar larvae of *E. phaeton* with large lateral black spots contiguous with the lighter spiracles on the abdomen from the fourth to tenth segment. While these spots are present in *E. euterpe*, they are greatly reduced in size and are remote from and not much larger than the black spiracle. Comparison between larvae of the Carrizo Plain *E. euterpe* population and *E. phaeton* shows this difference distinctly (Fig. 2). Fifth instar larvae of *E. p. phaeton* and *E. p. mojave* have two color morphs (green or pink). The black lateral spot on each segment is embedded in pink and/or green ground color. Additionally, *E. euterpe* has a prominent brown pattern on the dorsal and lateral surfaces.

SURVEYS AND DISTRIBUTION

PMJ conducted extensive surveys for adult moths at locations around the Carrizo Plain during the spring of 2003. The species was located along sandy washes in 2002, consistent with the habitat of the species at its previously known locality in Kern County. Survey sites for 2003 therefore were located by mapping gently sloping, sandy drainages within the Carrizo Plain National Monument with existing georeferenced data. From January through March, 20 potential sites were visited and surveyed at a slow pace to detect adult moths. These surveys produced three confirmed sites (two from 2002 and one new), two unconfirmed sites where moths were observed but identities could not be determined conclusively, and a description of other potential sites based on habitat similarities to confirmed sites.

The confirmed sites are located on washes flowing north from the Caliente Range and along the Elkhorn Scarp (Fig. 3). At the unconfirmed sites possible *Euproserpinus euterpe* adults were observed but determination of species was not certain. Potential sites that warrant further investigation based on presence of foodplant, geomorphology, and soils include the washes found along the northeast slope of the Caliente Range from Padrones Road to KCL Campground and the washes on the southwest slope of the Elkhorn Scarp from Latitude 35.055°–35.246° N to the Panorama Hills. Other potential sites are located outside the Carrizo Plain National Monument. The area to the northwest of the Monument was not explored.

We found potential sites that have been so degraded by agricultural use that the habitat cannot support the moth. Such sites include the washes flowing out of the Caliente Range into the Cuyama Valley. On many of the washes, the alluvial fans that would be prime habitat for the moth have been disked over and planted in various crops. Potential habitat has been replaced by agricultural uses in the washes flowing out of the hills east of Highway 33 between Highway 166 to just beyond the Ventura County line. (NB: The foodplant *Camissonia campestris* does not grow commonly south of this point and is replaced by a different *Camissonia* species.) These alluvial fans have been converted to agricultural use, but it is possible that a population of the moth could exist on a few of the lesser-used fans such as those around Ballinger Canyon Wash.

We identified sites that would be unlikely to support a population of *Euproserpinus euterpe* because of soil, geomorphology, or lack of host plants. These include the washes coming out of the northeast slopes of the Temblor Range, washes southeast of the Carrizo Plain National Monument that flow into the San Joaquin Valley, and washes surrounding the Elkhorn Plain, especially at the southeast sink.

FIG. 2. Euproserpinus larvae (length). Row 1: First instar *E. euterpe* (5 mm), third instar *E. euterpe* (12 mm). Row 2: Fourth instar *E. euterpe* (27 mm), fifth instar *E. euterpe* lateral (36 mm). Row 3. Fifth instar *E. euterpe* ventral (36 mm), fifth instar *E. phaeton* (35 mm).

NATURAL HISTORY

Phenology and Abundance. At two of the known sites, transect walks were conducted regularly throughout the flight season to gather additional information about the abundance and adult phenology of the species. Transect walks are the most effective method to gather information about the flight season that does not involve handling individuals (Pollard 1977, Watt *et al*. 1977, Thomas 1983). Mark-release-recapture studies should be avoided for listed, small Lepidoptera that may be harmed by handling (Gall 1984, Murphy 1988). Surveys were conducted as Pollard Walks, with the observer (PMJ) walking at a slow pace and recording every moth observed within a 5-m-wide area projected ahead of the observer (Pollard 1977, Thomas 1983). Temperature and other weather conditions were noted for each survey, and the location of each moth was recorded with a handheld Geographic Positioning System (GPS). To gain the maximum information from transect counts in subsequent analyses, transects were

FIG. 3. Range of *Euproserpinus euterpe* at Carrizo Plain. Shaded habitat region contains potential habitat with foodplant along sandy washes. Potential habitat on the south washes of the Caliente Range may extend farther to the northwest.

surveyed from the first detection of adults until no more were seen (Mattoni *et al.* 2001).

We analyzed capture records and observations of *Euproserpinus euterpe* from Walker Basin (Tuskes and Emmel 1981, Osborne 1999b) to compare them with the survey results from the Carrizo Plain. Over 90% of capture records or observations at Walker Basin were between March 13 and April 1. Even if one looks at the number of successful collecting trips and not the number of individuals taken, 75% of the trips were during this period. The earliest and latest collections were February 26 and April 6. Collectors usually

attempt to find particular species in places and at times when they are reasonably confident that the species will be found (Dennis and Thomas 2000). These records, therefore, should not be taken to be a complete description of the species' phenology at Walker Basin. They do, however, provide sufficient basis for an initial comparison.

The flight season for *Euproserpinus euterpe* at the Carrizo Plain in 2003 reached its peak almost two months earlier than the average for Walker Basin records (Fig. 4). Ninety-seven percent of Carrizo Plain observations were between January 27 and February 25, essentially completing the flight season before the date of the first collection record from Walker Basin. We suggest two explanations for the difference in phenology between the two populations. First, temperatures in late 2002 and early 2003 were much higher than usual, leading to abnormally early development for both plants and insects. The long-term average flight period at Carrizo Plain is likely substantially later in the year than observed in 2003. Second, the Carrizo Plain sites are at a lower elevation (640–840 m) than Walker Basin (1,060–1,100 m) and therefore temperatures will be higher earlier in the year, leading to an earlier flight season.

Behavior. *Euproserpinus* moths thermoregulate by basking on open ground in sandy washes or any other cleared area, including squirrel burrows and dirt roads (Osborne 1999b). Osborne (1999b) suggested that this behavior results in significant mortality where roads are frequently traveled. On warm days, moths will perch in the sandy washes, or less commonly in other cleared areas. When flushed, or when chasing after a flying insect, a moth usually will fly in a large curve 0.3-1.0 m above the sand for 15 m or more and return to sitting on the open substrate. Moths were never observed alighting on surfaces other than sand or clearings.

Adult moths did not nectar at flowers during any of the 2003 observations. Few nectar-providing flowers were available early in the flight season, but several species matured later in the season. Females were observed ovipositing early in the flight season before nectar was available. Nectar is not necessary for moths to survive or to complete their life cycle. We presume that adults will nectar; nectaring may extend the adult lifespan and provide energy for additional activity in

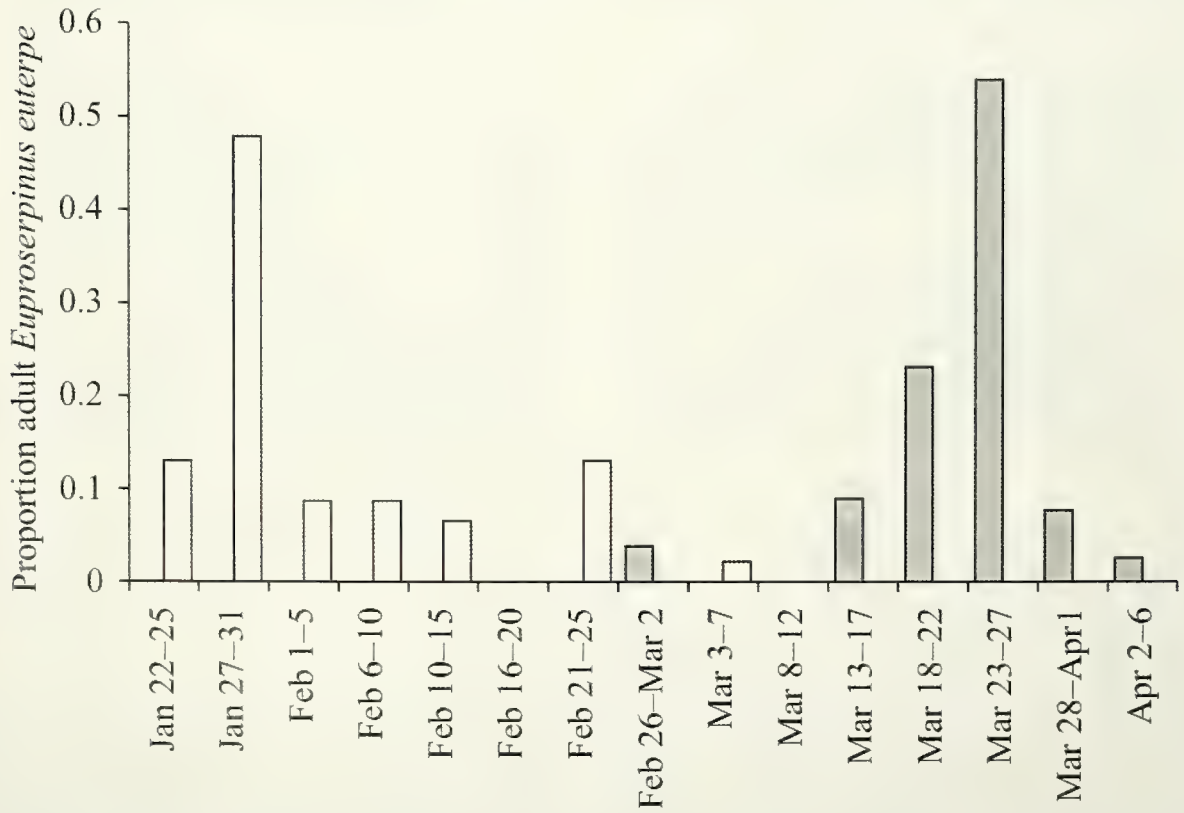

FIG. 4. Phenology of *Euproserpinus euterpe* at (a) Carrizo Plain (open bars) from observations in 2003 and at (b)Walker Basin (filled bars) from collections in 1974–1979 (Tuskes and Emmel 1981) and observations in 1999 (Osborne 1999b).

warmer weather, both of which increase opportunities for oviposition and thus may increase fecundity. *E. phaeton* commonly nectars on a variety of flowers (K. Osborne, pers. comm.) and P. Johnson (pers. comm.) documented *E. euterpe* nectaring at Walker Basin.

Reproduction and Larval Stages. Two female *Euproserpinus euterpe* were observed in egg laying behavior. One of the females laid one egg on a pebble and the second on a seedling (1 cm tall) of *Linanthus* sp. (Fig. 5). This egg was observed over several weeks, during which the plant dried up and finally blew away carrying the egg with it. To investigate oviposition and larval development, a single female was collected. This female was found with malformed forewings and was unable to fly. PMJ collected and placed her in a styrene box containing the host plant. Over the next several days she readily laid 75 to 100 eggs on facial tissue and less commonly on the host plant. This female is the source of the eggs and subsequently the larvae of this study.

On Carrizo Plain, larvae have been found feeding on *Camissonia campestris*, while larvae at Walker Basin are reported to feed on *Camissonia contorta epilobioides* (Tuskes and Emmel 1981), which is thought to be derived from a *Camissonia campestris* and *C. strigulosa* cross (Hickman 1993). *Camissonia contorta* is found at low density in the areas occupied by the moth at Carrizo Plain, mostly on the higher elevations of the washes, but it does not appear to be the primary foodplant. Other closely related sphingids use more than one species of Onagraceae as larval hosts (Osborne 1999a), so multiple hosts may be expected for *E. euterpe* as well.

First instar larvae exhibit the sclerotized thoracic shield and anal horn diagnostic of *E. euterpe*. Later instar larvae are brightly colored and patterned, which provides camouflage to blend in with surrounding plants, as suggested by McFarland (1966) and Osborne (1995). When feeding, later instar larvae exhibited a jerky side-to-side motion that resulted in the appearance of the foodplant and larvae being wind-blown (video available at http://www.urbanwildlands.org/kpsm.html).

Essential Habitat Elements. Sandy washes and other open soil are necessary for basking by adult moths on cool winter days. During 2002, over 40 specimens were flushed from sandy washes or lesser clearings such as those made by rodents, while no specimens were seen along dirt roads (primarily clay without sand) near or adjacent to washes. Day temperatures below 58° F

FIG. 5. Habitat of *Euproserpinus euterpe*. Row 1. Sandy washes showing cover of *Camissonia campestris* at Carrizo Plain, San Luis Obispo Co., CA. Row 2. Habitat at Walker Basin, Kern Co., CA (left), *Linanthus* sp. seedling at Carrizo Plain upon which *E. euterpe* egg was laid (right).

excluded any adult activity in 2003 observations. Between 58° F and 60° F, adults could be flushed from basking sites. Temperatures above 60° F were needed before "normal" activity occurred. On windy days these temperatures were slightly higher.

The foodplant *Camissonia campestris* appears to be essential for the Carrizo Plain population, although it is possible that other *Camissonia* species are used. *Camissonia campestris* is found abundantly throughout the Carrizo Plain but is somewhat restricted to sandy soils. Plants are most common within or on the banks of sandy washes where they can grow in monocultures of a square meter or more. Alluvial fans have been formed where washes flow out in the flatter plains. On these fans, *Camissonia* flourishes abundantly. These alluvial fans go through stages of succession gradually losing the sandy nature of the soil. On mature soils the *Camissonia* is less abundant than on immature sandy soils. Most of the patches of *Camissonia* do not appear to support populations of *Euproserpinus euterpe*, based on extensive surveys throughout the flight season. We presume that acceptable habitat is usually found along sandy washes with young alluvial sandy soils that support large patches of the foodplant. These conditions are often, but not always, found in washes with low or no banks. Despite many hours of searching, adults were never observed in the more mature soil types except in clearings caused by rodents despite many hours of searching in mature soils, but this does not rule out opportunistic use as basking sites of any small clearing near known localities. We also presume that the *Camissonia* must be sufficiently dense so that the plants are close enough for the newly emerged larvae to be able to locate seedlings and for larvae to locate additional plants when the original plant is consumed. Additional research is needed on this topic.

Sandy alluvial soils are necessary to provide sites for the mature larvae to burrow into the sand to pupate. We presume that if the soil is compacted the larvae may not be able to burrow. Older alluvial banks or fans are unsuitable for reproduction because the soil becomes too compact and loses the sandy consistency necessary for pupation. Indeed, Osborne (1995) found for the related species *Proserpinus clarkiae* that confined larvae would die without pupating if humid pupation sites were not provided. We presume that sandy alluvial soils located outside channels that are flooded yearly provide optimal habitat. This limitation in soil type would mean that most of the thousands of acres of *Camissonia* on the Carrizo Plain are unsuitable for the reproduction of the moth.

Predators and Parasites. No direct observations of predation or parasitism were made. Insectivorous birds, including horned larks (*Eremophila alpestris*), are common on the Carrizo Plain during the larval development period and may be predators. Predatory ground beetles (*Calosoma* sp.) also are present and active during the larval development period. The beetle is active on warm, sunny days, and hunts small soft-bodied insects. Several groups of wasps and flies that may be parasites of *Euproserpinus* are active during the early spring months. Predator ants of the genus *Formica* are common and active during the larval development period. Lizards may have an effect on the developing larvae but only *Uta stansburiana* was observed in the larval development areas.

DISCUSSION

The discovery of *Euproserpinus euterpe* at Carrizo Plain substantially extends the distribution of a species thought to be endemic to a narrow geographic range. Both populations share the morphological features that distinguish *E. euterpe* from *E. phaeton*. Future genetic analysis may provide greater understanding of the relationships between the populations of the two species.

Habitat conditions at Carrizo Plain are substantially similar to those at Walker Basin. At both localities, the moth uses annual *Camissonia* species as larval foodplant. Different foodplant species are apparently more important at the two locations — *Camissonia campestris* at Carrizo Plain and *Camissonia contorta* at Walker Basin. Current research is, however, inadequate to determine the use of additional *Camissonia* species at either location. Larvae from both the Carrizo Plain and the Walker Basin (Osborne 1999b) will eat other local *Camissonia* species if offered, without apparent ill effect. The moth lives in and around sandy washes with sandy alluvial soil at both localities. Both populations use plant-free areas for basking, including dirt roads at Walker Basin (Osborne 1999b). We made no observations of moths on roads at Carrizo Plain, although a road runs within 15–60 m of one site. This road is compacted smooth clay, while the roads at Walker Basin are sandy, so this difference is likely only one of substrate preference.

Disturbance and Dispersal. Little is known of the dispersal and colonization ability of *Euproserpinus euterpe*, nor the stability of populations over time. At the Carrizo Plain, one site seems not to have been plowed under for at least several decades, as suggested by the presence of mature *Ephedra* sp. bushes. In comparison, another occupied site was plowed under for many years before the early 1980s, which would have excluded the moth from the wash during that period. The near proximity of the disturbed site to the

undisturbed site leaves open the possibility that there has been recent emigration from one to the other. The soil conditions required by the species suggest an adaptation to movement into new habitats over the long term. We hypothesize that younger washes are necessary to provide appropriate soil conditions for the species, while older formations support consolidated soils and too few foodplants. It would be consistent with this habitat characteristic that the species is adapted to colonization of new habitats over the course of decades. This is a topic for future investigation.

More must be learned about the response of the moth to disturbance. Some disturbances, such as sheep grazing, are visibly deleterious to the species. Herds of sheep mechanically disturb soils and leave little forb cover, compared with the more solitary grazing behavior of cows. Grazing by sheep in arid landscapes increases soil compaction (Webb and Stielstra 1979), which is incompatible with maintenance of moth habitat. Sheep grazing suppresses biomass of native forbs, and excluding sheep grazing (along with excluding off-road vehicles) has shown to increase biomass of *Camissonia campestris* significantly (Brooks 2000). We observed washes in field surveys that had been grazed by sheep and turned into a muddy mess with little forb cover. It is not clear if this effect is permanent, but soil recovery from grazing is usually slow in arid environments.

Natural disturbances also affect moth habitat. For instance, following the 2003 field season, a freak summer storm flooded and silted in an occupied habitat. We have no knowledge of whether pupae are adapted to such events and emerge the following season, or whether they are adversely affected. Fires are highly unusual during the season of adult and larval activity. Clearing of vegetation by summer or fall fires would have an unknown effect. Based on behavior of captive larvae of *E. phaeton* (N. McFarland, pers. comm.), we believe that most pupation will occur deep in the soil. Tuskes and Emmel (1981) stated that *E. euterpe* larvae pupated near the surface but did not describe whether sand was provided for larvae to burrow deeper. Additional studies are necessary to determine how deep and where larvae pupate in nature. If pupation takes place near the surface, then summer and fall fires could be detrimental. This would probably only affect those larvae that migrate from washes and clearings into denser vegetation to pupate; by summer and fall, most *Camissonia* patches do not have sufficient fuels to maintain a fire.

***Erodium* and Larval Survival.** Tuskes and Emmel (1981) reported that female *Euproserpinus euterpe* frequently oviposit on the exotic annual *Erodium cicutarium*. Larvae they reared on *Erodium* in the laboratory did not feed and died within three days. Tuskes and Emmel (1981) hypothesized that because first instar larvae are "rather sessile" those larvae hatching on *Erodium* in the field are likely to die. This assertion has been widely repeated and forms the basis for the conservation strategy articulated for the species (U.S. Fish and Wildlife Service 1984). We (Longcore and Rich 2002) suggested that the first instar larvae are sufficiently mobile in the field to seek out palatable foodplant if plants are sufficiently closely spaced, which seemed possible because first instar larvae already move from oviposition sites on leaves and stems to flowerheads where they prefer to feed (Tuskes and Emmel 1981). In captive rearing, PMJ observed first instar larvae to move from plant to plant, suggesting that this also would be possible in the field. First instar larvae of many Lepidoptera species are capable of moving significant distances, and this ability is not proportional to body size (Reavey 1992). In an investigation of 42 Lepidoptera species, first instar larvae could live 1–20 days without food, with movement ability ranging 0.7–267.8 cm/hour (Reavey 1992). If suitable host plant is nearby, movement of first instar *Euproserpinus euterpe* larvae from nonpalatable plants to host plants is highly likely.

Some Lepidoptera, typically those with common host plants and those that diapause as eggs, do not lay their eggs directly on the host plant (Wiklund 1984). The effort to locate and oviposit on a common foodplant is wasted, while species with rare foodplants must locate eggs on them. In years with sufficient rainfall, *Camissonia campestris* is common, forming continuous beds in appropriate habitats at Carrizo Plain (Fig. 5; Row 1). The female moths we observed laid eggs on a pebble and a non-foodplant, showing no strong preference in oviposition choice at the fine scale. If eggs are laid on inanimate objects, it is unlikely that oviposition on nonpalatable plants is a maladaptive behavior. Females do not need to lay eggs directly on a common foodplant because neonate larvae hatched from eggs laid in the vicinity will have a high probability of encountering a foodplant.

We conclude that eggs laid on *Erodium* are not doomed, and that this exotic species does not present the negative population pressure once imagined. While we do not dispute that attempts to rear larvae on *Erodium* in the laboratory would fail, we discerned a greater ability of first instar larvae to move from plant to plant than previously observed (Tuskes and Emmel 1981). This revised interpretation is more consistent with current knowledge of the timing of *Erodium*

invasion in California. Research indicates that *Erodium cicutarium* invaded California from Baja California before the Mission period (that is, before 1769), and therefore invaded without disturbance from agricultural grazing (Mensing and Byrne 1998, Mensing 1998). *Euproserpinus* moths have persisted in landscapes with *Erodium cicutarium* for over 250 years and the introduction of this invasive species has likely reduced overall foodplant availability. This presumed reduction in *Camissonia* dominance seems the likely mechanism for any potential adverse effects on *E. euterpe*, not oviposition on *Erodium* itself as suggested by Tuskes and Emmel (1981).

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THE WINTER ECOLOGY OF *COLIAS EURYTHEME* BOISDUVAL (PIERIDAE) AND ITS DEPENDENCE ON EXOTIC LEGUMES IN SOUTHERN NEW JERSEY.

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ABSTRACT. *Colias eurytheme* adults were seen by 12 April in all of twelve years with observations near Delaware Bay in Cumberland County, New Jersey. Adults can occur in all months but successful reproduction is virtually impossible from mid November until very late February or March. Second through last instar larvae and pupae can survive local winters (January mean ca. +1.4°C). Pupae and most larvae overwinter without diapause. Survival outdoors for reared lots was 50% for second instars and 71% to 100% for older larvae and pupae. Larvae fed, grew, and molted over winter. Larvae deprived of food in December died in January. Nonnative legumes, especially vetches, provide essential food for larvae in autumn and winter, and the establishment of *C. eurytheme* in New Jersey apparently coincided with that of vetches. Lack of diapause allows for an earlier start in spring and an extra (sixth) annual generation combined with exceptional cold hardiness of larvae and pupae pre-adapted this species to exploit anthropogenic habitats with exotic cold season legumes where winters have some mild days and a January mean near or above freezing. The *"ariadne"* phenotype in spring is reliable evidence of local overwintering as late instars or pupae. Overwintered second instars produce summer form adults more than a month later. Southward movement was observed in two autumns and to an unknown extent *C. eurytheme* is a two way migrant.

Additional key words: *Viccia, Coronilla varia*, exotic foodplants, cold tolerance, *Problema bulenta*.

The orange sulphur (*Colias eurytheme* Boisduval) is often the most common butterfly in non-drought summers in Cumberland County, New Jersey, and is usually the most commonly seen butterfly from October through February. In a few decades in the mid 20th century this species became one of the most common butterflies in the eastern United States. At a time when many native Lepidoptera are declining as their habitats are being disrupted, overrun by alien weeds, eaten by out of control deer, or obliterated by development, the orange sulphur is a spectacular ecological success. It is the only native butterfly to occasionally reach pest status in eastern North America. Most authors now realize that immigrants from farther south repopulate the northern portions of its range each summer. Ferguson (1955) was perhaps the first to realize *C. eurytheme* is only a summer immigrant northward, specifically in Nova Scotia where the first worn immigrants appear in June or July. Ferguson (1991) also considered it a migrant that has reached Bermuda. Shapiro (1967, 1974) recognized this species as a late spring immigrant in central New York. However, the overwintering limits of the Orange Sulphur are poorly understood (e.g. compare maps by Scott, 1986 and Opler, 1992) and the literature is inconsistent as to whether larvae or pupae or even adults overwinter. Scott (1986) reports larval overwintering for almost every North American species of *Colias* including this one, and pupal overwintering for none. Harry (2005a,b) explicitly mentions overwintering larvae of five *Colias* species, including *C. eurytheme*, outdoors at West Jordan, Utah. However, many authors at least as far back as Klots (1951) claim *C. eurytheme* pupae overwinter. Shapiro (1967) demonstrated that pupae can withstand chilling for at least four weeks, but he was unable to overwinter larvae in a refrigerator. He suggested that pupae and possibly some mid instar larvae overwinter near Philadelphia, Pennsylvania, and reported adults as early as late March (1966, 1970). However he provided no direct evidence regarding overwintering stages outdoors and he (1967) noted a 33% incidence of cripples among adults from pupae chilled for only three or four weeks, about a third as long as a Philadelphia winter. I address overwintering ability of larvae and pupae under actual outdoor conditions less than 100 km farther south.

Winter populations of *C. eurytheme* near Delaware Bay in Cumberland County, New Jersey are almost certainly bolstered by progeny of immigrants from the north, whose southward progress may be blocked by the Bay. From 25 September to 4 November 1988 I recorded approximate flight directions for 51 *C. eurytheme* observed in sustained flight: 48 were headed south-southwest, two southeast, and one northeast. One female was observed to descend from above a several thousand hectare forest into a field, make five oviposition sequences, reascend over forest on the other side and continue on her southeast course. On 18 September, 1997 while driving I saw over 100 flying south-southwest across roads in Salem County, New Jersey, Cecil County, Maryland, and Chester County, Pennsylvania. Both sexes sometimes fly over forests, apparently to maintain direction, but will also often deviate from course to follow roads or powerlines heading generally south. Distances covered are unknown, but their flight is faster than that of a Monarch. Scott (1986) also reports a southward

movement in Manitoba and speculates that movements of this species are probably large but not those of a strong migrant. Females reaching Cumberland County in September and October will find good conditions for reproduction unless drought curtails autumnal greening of alien vetches, which are now the primary foodplants locally. However, low temperatures slow growth in autumn and on 5 December the average daily maximum falls below 10°C and remains so through 7 March.[1]

METHODS

Field observations were made in appropriate habitats in 1989 and 1995–2005, mostly about 2 km below Dividing Creek and at Port Norris, Cumberland County, New Jersey and occasionally farther inland in the same Townships. Reared larvae and pupae were observed in my yard at Port Norris, about half a km north of the Delaware Bay salt marshes, less than 10 meters above sea level at 39.2° North Latitude, where the January mean is about 1.4°C.[2]

During the winters of 1988–1989 and 1990–1991 I overwintered reared larvae and pupae of *Colias eurytheme*. Staggered sibling lots from females collected 29 October 1988 and 31 October 1990 were started outdoors beginning about 20 November; many were moved to a cool indoor room in early December. Larvae were fed potted white clover (*Trifolium* sp.) and whether indoors or outside all were kept under strictly ambient light. Those indoors were at mostly 13–20°C with bright indirect sun, but were placed outside two or three times per week on subfreezing nights to mimic late November conditions. A thin transparent nylon cover was usually placed on pots containing fourth or fifth instars during warm weather and on all indoor containers. Various instars were placed outside for the winter in December to as late as 1 January. Larvae that were first or second instars on 31 December 1988 had been reared entirely outdoors. Eight newly formed pupae and two prepupae were placed out in late January 1989. In 1990 I was able to obtain pupae earlier (Table 1). Larvae that year were sorted by instar and placed out on 3 December, but about five of the 41 "third" instars molted by 31 December.

[1]Climate data were obtained from The Weather Channel Website visited January or February 2005. Fahrenheit temperatures were used and converted to Celsius to one decimal place.

[2]There is no weather station on the New Jersey side of lower Delaware Bay. The mean at Millville, about 20 km north of the study area, is 0.3°C, but Port Norris minima are commonly 5°, and occasionally 10°C, warmer than at Millville on clear, calm winter and spring nights; temperatures are otherwise similar. Wildwood, with a January mean of 1.4°C, is probably more representative for winter, but that locality is much colder on spring afternoons.

Flower pots containing larvae were kept over winter in the outside corner of a large screen porch, about 3 meters from the house, for protection from birds, mammals and various winter-active invertebrates like ants and spiders. At that corner both sides were screen from floor to ceiling so larvae were fully exposed to ambient temperature, and partial mid-day sun. Since they were about a meter off the ground they probably experienced lower temperatures and perhaps more wind than they would have at the soil surface in nature. Except for one containing ten third instars in 1988–1989, all flower pots containing larvae were placed in my garden for all freezing precipitation and associated rain, and for most relatively light rain storms, but not heavy rains that might have flooded them. Most larvae were released in March since I did not have time or food resources to rear large quantities. The few that were reared to adults in the porch are now in my collection. In December 1990, 20 third instars were allowed to run out of food to determine whether winter feeding is essential. Their soil was kept moist and they were moistened with a plant mister on mild days to prevent dehydration. They were not exposed to snow and ice.

Except for the two lots previously noted, larvae were in direct contact with light snow and ice repeatedly and were snow-covered several times for up to two days in both winters. The maximum snow depth was about 6 cm. Most had moisture on or contacting them freeze overnight or longer, although none were encased in ice. Larvae were exposed to one minor ice storm each winter. The lowest temperature at Port Norris was about -15°C in January 1989 and about -12°C in 1991, but no periods longer than two days below freezing occurred in either winter. Periods of a week below freezing occurred in about half of the years when field observations were made. Snow cover of four weeks or more occurred starting in January 2002 and 2003, and the ground was snow covered for a week in January 1996.

For those pupae that could be safely removed, small pieces of the original substrate (usually the nylon cover) with a pupa attached were stapled on the underside of low vegetation, either in grass clumps or on the underside of *Plantago* rosettes (fairly typical pupation sites in nature), or were stapled to the underside of bamboo leaves on short stems and inserted in the soil at the edge of grass clumps. All pupae were about 2 to 4 cm above the soil and not exposed to direct sun. All pupae were moved to the screen enclosure on 5 March 1989 and 15 March 1991 and placed out of direct sun. Pupae formed on the flower pots were left in place and stored with the larvae. All pupae were outside within 12

TABLE 1. Pupation and eclosion dates for overwintered pupae of *Colias eurytheme* at Port Norris, New Jersey.

Pupation date, location	Eclosion dates 1991	Sex
on flower pots		
18 December	31 March	Male
23 December	8 April	Female
24 December	7 April	Male
2 January	9 April	Male
5 January	7 April	Female
8 January	10 April	Male
in garden		
15 December	8 April	Female
17 December	6 April	Male
19 December	3 April	Male
19 December	7 April	Male
19 December	9 April	Female
20 December	9April	Female
21 December	9 April	Male
21 December	11-15 April	Female
27 December	9 April	Male
29 December	11-15 April	Female
31 December	11-15 April	Female
3 January	10 April	Male

hours after pupation and remained there until eclosion. Pupae attached to the flower pots received substantially more direct sun in winter and the plastic surfaces warmed noticeably, causing eclosion to be a few days earlier than those kept in the garden. Therefore their eclosion dates were analyzed separately. Spearman rank correlation tests were performed by L. F. Gall, using SAS software version 6.04 (with the correction for ties). Chi square tests were done by the author on a hand calculator. Forewing measurements were taken on the left forewing from the mid-basal point to the apex using an ordinary ruler and rounded to the nearest mm.

RESULTS AND OTHER OBSERVATIONS

Field observations. From 1995 through 2005 I collected adults, nearly always fresh and often teneral near their pupal shell, on warm (usually >16°C) days in January (17 in five different years with 12 in 2000), February (18 in four different years), and March (25 in seven different years) at Dividing Creek or Port Norris, New Jersey. I saw a few dozen others from 28 February to 31 March, especially in 1998. The fact that I rarely encountered worn adults in January and February probably reflects avian predation. They are so conspicuous while basking that I can sometimes spot them at >30 m and surely birds can do better. Winter adults are very cold hardy and a night in the freezer (ca. -15°C) does not reliably kill them. Shapiro (1967) found that most unfed adults could survive more than a month at 3°C. Although slightly subfreezing nights are harmless to all stages, a single frigid period and perhaps prolonged cold probably can kill pupae that are close to eclosion. Usually after a night below about -12°C several warm (>15°C) days must occur before adults are seen again. An extreme case occurred in late 2004. Adults were seen flying on mild days into mid December but on 20 December 2004 the afternoon high reached only -8°C with strong winds and two mornings were about -12°C. Most winters do not have any days that cold. Several days exceeded 10°C later that month, and 31 December through 14 January were completely frost free at Port Norris (two days reaching 18°C). Maxima were 15°-16°C on 8 and 16 February 2005. No observers saw any sulphurs locally after 20 December 2004 until 30 March 2005 (Damon Noe), although I visited reliable fields on the four warmest winter days. Since 1989, the start of major spring flights (several patrolling males per hectare in good habitats) has varied from 26 February in 1998 to 12 April in 2003 at Dividing Creek. I also found a wandering last instar larva there on 22 February 1998, which I fed clover. It attached on 5–6 March, yielding an "*ariadne*" form male

on 17 April. These field observations indicate that both larvae and pupae overwinter locally.

Field collected males were 90% *"ariadne"* (=*"vernalis"*) phenotypes in January (n=10), 100% in February (n=12), and 94.4% in March (n=18). This form occurs into mid April. Although placement of some females is difficult, I would consider all of 12 February and March and six of seven January females to be spring phenotypes. The *"ariadne"* phenotype is small with reduced orange, often as little as on the Texas male illustrated by Opler (1992). The black border is pale, usually narrower than in Klots' (1951) illustration or even fragmented on males, and in February and especially March (22%) the forewing black border may be nearly limited to the apical region. A few have the discal spot reduced to a ring on the forewing. Some males show a row of weak dark postmedian spots on the forewing above, as is discernable on Hoffman's (1973) Fig. 1C. A heavy basal black shading dorsally sometimes expands to infuse most of the hindwing on females. Ventral hindwings are always infuscated. While summer form males rarely have forewing lengths below 25 mm, 40 males field collected from January to March range from 17 to 24 mm, with the means 21.0 mm for January, and 20.2 mm for both February and March. Much smaller specimens are known (e.g. Shapiro, 1996, Anthony McBride, pers. comm., 2005). Forewing length of nine of my 30 February and March males are under 20 mm as is one of ten collected in January. A newly eclosed non-*"ariadne"*, dorsally nearly summer form, male collected 20 January 2005 is also small (forewing length 22 mm). Klots (1951), Ae (1957), Hoffman (1973), Scott (1986, Plate 12, fig. 37), Iftner et al., (1992, p. 190 bottom center), and Opler (1992) illustrate *"ariadne"* males, but I suspect the Iftner et al. spring female is a hybrid. These forms overwhelmingly predominate from January into April whether or not *Colias philodice* Godart was present the previous fall. Ae's and Hoffman's stocks came in part from places where *C. philodice* is quite rare. Thus, old suggestions that these forms are hybrids are untenable.

Adults were seen and sometimes collected in December in all years from 1994 to 2004, but not in 2005. Most November and December adults are summer phenotypes except for more black dusting ventrally (consistent with Hoffman, 1973, Fig.3) and usually at least basally above. I have also collected *"ariadne"* forms in late November and December (especially in 1998), although these are usually larger than those collected from February to April. Whether they mate and oviposit or not, adults in mid or late November through most of February obviously do not produce surviving offspring. Eggs laid 1–10 November require at least 20 days to hatch based on observations in three different years. Larvae from eggs laid later would usually have inadequate time to reach the second instar in cool December conditions.[3] Eggs laid in December almost never hatch, based on observations in 1988, 1990, and even the extremely warm December of 1998. Emigration of adults in mid November through December is virtually precluded by low sun angle and temperature[4], such that conditions for sustained flight occur infrequently and for less than four hours per day, and usually with a substantial southwest wind.

Survival and other observations of larvae and pupae. Survival to 15 March 1989 was 50% for larvae placed out as second instars (n=20), 71% for third instars (n=17, excluding one I crushed and two escapees) including four of seven protected from snow and ice and eight of ten exposed larvae, 100% for fourths (n=10). All 8 pupae eclosed 11–16 April. Both prepupae died in February. All surviving larvae had molted by 15 March. None of about 20 that were first instars in mid December survived through January although a few died as early second instars. As of 5 March 1991, survival was 98% for thirds (n=41), 100% for fourth and fifth instars (n=5), and 86% of pupae (n=21). These pupae eclosed from 31 March to 15 April (Table 1). Most larvae molted in February and all third and fourth instars except the two discussed below had molted or were in molt by 5 March. Some of these had also molted in December. Harry (2005b) states that his larvae resumed feeding 24 February in Utah. None of the 20 third instars that ran out of food in December or 29 first instars survived through January 1991. None of approximately 20 unhatched eggs survived past early January in either year. One last instar larva was dislodged in a storm and submerged in about 2 cm of near freezing water for five to twelve hours, but recovered and produced an adult. All three pupae that died had become partially dislodged and imbedded in the soil. The immediate cause of death appeared to be bacterial sepsis, with two deaths in March. Survival of second and third instars in 1989 does not differ significantly (χ^2=1.6), nor do fourth instars and thirds (Fisher's exact p=.124). However, seconds and thirds pooled do differ from fourths (χ^2=5.95, p<.025), suggesting that in some winters older larvae may fare better. All mortality of third instar larvae in both years was associated with interruptions of molts by cold spells

[3]The mean for 1 December is 5.0°C dropping to 1.1°C by the 31st at Millville, New Jersey.

[4]Given low wind and full sun the minimum for sustained patrolling by males is about 17°C in December-January falling with increased insolation to about 4°C in mid April in Cumberland County, New Jersey at 39.2°N.

which extended some mid-winter molting periods to nearly a month. Four died in pre-molt and two died while being unable to feed after molting.

Larvae fed on days that reached 9°C, and on sunny days as cold as 6-7°C.[5] First to third instar larvae remained on the upper surface of the clover leaves most of the time, and these leaves probably act as miniature parabolic reflectors on sunny days. Third instars often left the foliage when the air temperature fell to 4°C, especially if this happened in the daytime. Older larvae rested on stems or on the soil. In both years most larvae overwintered without diapause and were observed to feed and molt. However, two third instars in 1990–1991 were much less active than the others but occasionally moved a few cm. They apparently did not feed in January or February, and appeared to be in diapause. Both were actively feeding, but still third instars, on 5 March and were not tracked separately after that date.

Spring 1991 eclosion dates (Table 1) were significantly coupled with pupation dates: r=.882, p=.02 for garden males, r=.929, p=.008 for garden females (but note ties), and r=1, p<.05 for males in flower pots. Coupling of pupation and eclosion dates indicates that pupae developed during warm periods in winter and were not in diapause. Exposure to warmth, and therefore eclosion dates, varied as a function of pupation dates. Maximum daily temperatures were 16–18°C on 18, 21 (the median pupation date), 22, 23 December 1990 and 20°C on the 30th but then remained below 10° C through 14 January 1991. Wild adults were observed six and three days before my first eclosions in 1989 and 1991, again verifying pupal overwintering in the field, presumably from pupae formed before December.

Adults from overwintering pupae were 96% vernal form *"ariadne"*, as were those from overwintered last instars. A few overwintered third instars were reared to adults. Eclosions started 30 April 1991 and 6 May 1989. Adults were nearly as large as wild summer adults, and the three males were close to summer forms, while the four females had reduced orange. Such intermediate phenotypes would be expected based on Hoffman (1973, Figs. 3, 4), since they were at about 11 hour days as late third instars[6] , and about 12 hours as late 4ths. Transitional phenotypes usually appear in late April, with the males close to summer phenotypes dorsally. Two larvae that were second instars on 1 January produced slightly small summer form males on 16 and 20 May 1989, 35 and 39 days after their first sibling eclosed from an overwintered pupa. Wild adults of similar phenotypes were seen 20 May.

DISCUSSION

The results directly demonstrate that not only pupae but also second instar and older larvae of *Colias eurytheme* can survive winters in southernmost New Jersey without diapause. Results from 1989 suggest later instar larvae probably fare better on average than second and perhaps third instars. Shapiro's (1967) larvae could not survive the winter when refrigerated at 3°C, yet I report 50% survival of second instars and 71-100% survival of older larvae and pupae under seemingly much harsher winter conditions (roughly -15°C to + 18°C). Wild larvae and pupae in many years encounter periods of a week or more of continuous freezing. Since no diapause is involved, I doubt survival differences are related to rearing conditions prior to chilling. My larvae were reared at natural late autumn photoperiods mostly below 20°C with frequent freezing nights. Many of my last instars in December showed the dark patches characteristic of short-day larvae. Shapiro's refrigerated larvae were continuously below the threshold for feeding. My outdoor larvae were able to feed several times in January and often enough to grow during February when many went into successful molts. Some larvae molted twice outdoors between 7 December 1990 and 5 March 1991. The failure of my larvae to survive outdoors without food suggests Shapiro's refrigerated larvae also died of starvation. Furthermore, adults from four of 12 pupae in various stages of development that Shapiro chilled for 21 or 28 days were at least slightly crippled. Out of my 26 adults from overwintered pupae, one failed to recover and expand after a fall, but none of the other 25 were defective. Probably expressing the small, less pigmented *"ariadne"* phenotype effectively reallocated resources among my pupae.

Colias eurytheme overwintered annually in all years with observations, specifically 1989 and 1995–2005, near Delaware Bay in New Jersey, where the January mean is about +1.4°C. This included one very cold winter and two with persistent snow packs. Substantial numbers were flying by mid March in three of twelve years and by 12 April in all years. Occasional adults eclosed in mid winter in some years, especially in January 2000. Shapiro (1966, 1967) considered overwintering to be reliable about 100 km to the north in and immediately adjacent to Philadelphia, Pennsylvania (January mean 0°C). Shapiro (1974) reported adults as rare in mid April, which I would interpret as pupal survival, and more regular after 5 May, which indicates larval overwintering, slightly to the northeast on Staten Island, New York City (January

[5]The mean maximum for January at nearby Millville is 5°C.
[6]At 39° North day length reaches 11.0 hours about 21 February.

mean between -0.3 and +0.3°C). The January mean at Harry's (2005b) Utah site is also about -0.3°C. Overwintering of pure *C. eurytheme* is rare (and usually as larvae) or does not occur at all in places where the January mean is below about -1°C such as west central Illinois (Sedman and Hess, 1985), Ohio (histogram in Iftner et al., 1992), central and northeastern Pennsylvania (Thomas Manley, pers. comm., March 2003, David Wright, pers. comm., February 2005), central New York (Shapiro, 1974), Massachusetts (personal observations: none seen before June in 1973, 1974, 1984-1988), and Connecticut, (personal observations 1975-1983 and Connecticut Butterfly Atlas Project data). Shapiro (1974) states early spring (May) orange sulphurs in central New York are almost always male hybrids, as were two of five orange spring sulphurs I collected 30 April to 17 May in milder southern New England. Apparently at least one (the female illustrated by Iftner et al., 1992) of about 13 records through 15 May in Ohio is a hybrid. *C. eurytheme* populations in and north of those regions appear to depend on annual immigration. While the first pure *C. eurytheme* adults seen in these colder regions are usually summer phenotypes in late May or June, the first adults along Delaware Bay in New Jersey are *"ariadne"* phenotypes in or before early April.

An apparently reliable indicator of successful overwintering of *C. eurytheme* as pupae or late instars is the occurrence of the small early spring phenotype. Transitional phenotypes, especially relatively large females with reduced orange, are probably reliable indicators of third or fourth instars overwintering. The *"ariadne"* phenotype is known to be induced by short photoperiods during the third and fourth instar (e.g., Ae, 1957[7], Hoffman, 1973). Larvae overwintering as third instars would mostly be late fourths or fifths at the vernal equinox in southern New Jersey and produce adults in late April with more normal borders in males, but reduced orange in females, and some dark frosting beneath. Larvae that overwinter as second instars would be third or fourth instars at the time of the vernal equinox, and produce essentially summer phenotypes. Virtually all more western regions, including Utah, where *C. eurytheme* overwinters, warm up earlier than southern New Jersey. Farther north if the few diapausing third instars were to survive the winter (which is purely hypothetical) they would probably resume development near the vernal equinox meaning that for much of the third instar and all of the fourth they would experience long and increasing photoperiod resulting in essentially summer phenotypes. Since they do not occur that late farther south, rare *"ariadne"* forms in May northward probably come from locally overwintered last instars or pupae such as produce this phenotype in New Jersey. Furthermore, small early adults from local colonies, seldom disperse from their natal field, and certainly do not migrate. Larger transitional phenotypes with reduced orange in females and relatively normal borders in males (such as those I reared from overwintered third instars) often occur into early, but not late, May in southern New Jersey and commonly disperse along roadsides. While the possibility of immigrants of these transitional phenotypes appearing northward during warm weather cannot be ruled out, Shapiro (1974) and Sedman and Hess (1985) are certainly right that the first immigrants northward are usually summer forms in or after late May.

Expression of the *"ariadne"* phenotype may be exaggerated directly by environmental factors, but since neither Hoffman (1973) nor Ae (1957) examined phenotypes produced by larvae or pupae below 15°C, further modification of genetic expression by cold cannot be ruled out, and might be expected if functions of this phenotype include reallocation of resources under harsh conditions. Size as measured by wing length, width of male forewing border, and ventral reflectance are photoperiod controlled with the last gradually reduced by decreasing day length below 14 hours. Ae (1957) found no difference related to photoperiod in the intensity of orange but did in its extent. Overall my February and March adults have less orange than those from any other months. Wild adults then are smaller than Hoffman's or Ae's laboratory adults or my December *"ariadne"* specimens. Cold during pupal development might directly affect extent of orange pigment, black pigment in borders, and discal spots, producing the extreme phenotypes in February and March. Nutritional stress and cold acting on last instar larvae in November and December probably result directly in additional dwarfing beyond reduced size induced by photoperiod, and dwarfing is possibly exacerbated by resource depletion of pupae over winter. Between necessary cryoprotectants and respiration, metabolic costs of overwintering in insects are substantial, and resource depletion is a real possibility (e.g. Leather *et al.*, 1993, Chapter 5) and might be especially high for developing (as opposed to diapausing) pupae. Wild adults in winter and early spring also often have slightly malformed wings including one of fifteen January, four of seventeen

[7]Ae has no statistical analyses, but for broods P-78-4 through P-78-8 five paired comparisons of 14 hour vs.10 hour photoperiod treatments show no overlap in the average forewing lengths or "black-border index" among males so U=0, n1=5, n2=5, p=.004. Similarly reduction of orange seems obviously different by inspection at least for males.

February, and three of 25 March specimens in my collection. This is consistent with Shapiro's observations with pupae chilled for 21 or 28 days. My 25 adults that eclosed from 31 March to 16 April had no such defects, perhaps reflecting relatively mild artificial conditions as last instar larvae or warmer temperatures late in the pupal stage than experienced by wild adults eclosing earlier.

Two larvae reared in natural photoperiod and placed outside in December as third instars apparently diapaused, and winter larval diapause is widespread in this genus. This begs the question of why a higher incidence of winter diapause is not selected for in *C. eurytheme*. Diapause would eliminate wasting of adults from late autumn and winter eclosion, as well as winter mortality of eggs, first instars, and prepupae. Probably diapause would improve survival of larvae in northern winters, but diapause may be disadvantageous southward and immigrants would swamp progeny of northern survivors by June. In southern New Jersey for larvae in the third instar at the onset of winter, the chance of survival is probably better with diapause if the food supply fails, but most years survival is probably not much different with or without diapause and survival prospects are probably improved by reaching the fourth or fifth instar by December rather than diapausing. Along Delaware Bay not diapausing essentially allows an extra generation for those that reach last instars or pupae by December. From about early June into mid September[8], a generation can be completed in about a month (Scott, 1986, Gochfeld and Burger, 1997). Second brood offspring of early adults eclose in late May or early June, so there is time for a partial sixth brood by mid October. This last brood is protracted by cool weather, bolstered by immigrants from the north, and probably depleted by south-bound emigrants. In non-drought seasons each brood usually outnumbers the last, so an extra brood should cancel moderate losses of ill-timed stages in late autumn and winter. Regardless of when prolonged cold sets in, most individuals should be in stages with the potential to overwinter. Winter losses are probably lower farther south. In the Carolina and Georgia piedmont, adults can probably successfully reproduce through November in years without early extreme cold and successful reproduction should be possible for adults eclosing in late February in most years[9]. Coastal plain portions of these states have average daily maxima of 11–15°C even in January so, despite some periods of cold weather, *C. eurytheme* could potentially breed nearly year round if suitable winter foodplants were available.

[8]This is the period when the mean temperature is 20 to 25°C at Millville, New Jersey.

The phenology of *C. eurytheme* has apparently changed very little in Connecticut, just north of the reliable overwintering zone, during the 70 years since it became common. The first known spring *C. eurytheme* adult was collected 16 May 1939, and as I interpret the Connecticut Butterfly Atlas data, there are apparently only three subsequent early collections or observations of more than one individual, four specimens collected 1 May 1954 (at Yale University), three on 30 April 1983 (my collection), two seen on 10 May 1994, and only about 16 singletons. These spring records include some hybrids. Likewise, adults were occasionally found in early December in both the 1930s and the 1990s.

I have no well-documented information on the local winter ecology of the allegedly native *Colias philodice*[10], so it is impossible to conclude whether or not introgression has affected the winter ecology of either sulphur. Since 1990, *C. philodice* has varied from zero to about 15% of summer *Colias* observed in southern New Jersey. This species is also apparently somewhat migratory (Ferguson, 1991; Gochfeld and Burger, 1997) but is considered to overwinter in almost all of its range (e.g. Scott, 1986, Opler, 1992, Ferguson, 1955) and its shorter flight season suggests a diapause. I have seen only one adult in November, and I know of no credible observations (including 114 specimen dates, some of which refer to more than one specimen, compiled by David Iftner) of *C. philodice* from 12 November through 26 March in New Jersey. The spring brood peaks and declines rapidly in April (see also Iftner et al., 1992) suggesting a single overwintering stage, probably the fourth or fifth instar larva.

Johnson (1995) concludes that none of the ten southern migrant moths and Homoptera (nine apparently with no diapause) that he reviewed overwinter as far north as the 0°C January isotherm and only three do so above the 4°C isotherm. This is consistent with maps by Opler (1992) for a number of southern migrant butterflies and skippers. Similarly, *Pseudaletia separata* (Walker) (Noctuidae) larvae and

[9]The daily mean falls below 10°C on 29 November at Atlanta, Georgia and 23 November at Raleigh, North Carolina compared to 6 November at Millville, New Jersey. However -10°C or lower has been recorded as early as 23-25 November at all three locations. but such cold is rare before late December. The daily mean reaches 10°C on 26 February at Atlanta, 13 March at Raleigh, and 8 April at Millville. The latest recorded dates for -10°C or lower are 5 March at Atlanta, 14 March at Raleigh, and 22 March at Millville.

[10]If some stage can reliably reach diapause by October or survive six months with no food, native *Baptisia*, *Lupinus*, and *Tephrosia* might have supported this butterfly, although *Tephrosia* is not a known foodplant for any *Colias*, and *Lupinus* (now rare) often senesces in July or August. *C. philodice* has been established at nearby Philadelphia since at least 1833 (specimens in Titian Peale collection, Academy of Natural Sciences, Philadelphia).

pupae can overwinter, apparently without diapause, in portions of China where the January mean is at least 0° to 4°C (Hirai, 1995, Johnson, 1995) and the moths migrate into a much larger summer range. Orange sulphur larvae and pupae are obviously more cold tolerant than these other non-diapausing migrants, except perhaps *P. separata*, and apparently of very similar hardiness to diapausing adults of the migratory noctuid *Plathypena scabra* (Fabricius), which also overwinter abundantly in southern New Jersey (my observations). While places with a higher January mean often have extreme minima comparable to southern New Jersey[11], there are more warm days for feeding during winter, which may be essential for these species. Places with a January mean near 0°C typically have an average daily maximum of 10°C, which is warm enough for larval feeding, into early December and again by late February or early March. A few warm (10–15°C) days usually occur each month even in mid-winter, which is adequate for *C. eurytheme* larval feeding. With increased insolation and slightly higher temperatures some larval feeding is possible for *C. eurytheme* even on near average afternoons by mid February in southern New Jersey. Several Noctuinae such as *Abagrotis, Agnorisma, Xestia* and *Eucoptocnemis* species also overwinter as larvae near the ground in southern New Jersey and feed, grow, and molt as weather permits during the winter. The geometrid, *Nemoria lixaria* (Guenee), overwinters locally as intermittently active larvae feeding on red maple (*Acer rubrum* Linnaeus) buds and flowers, based on two late winter field collections and several reared broods. None of these moths are considered migratory and the noctuids range into much colder climates but, like *C. eurytheme*, *N. lixaria* is near its limit for winter survival and apparently became established in Cumberland County recently (1980s).

Importance of exotic legumes to *Colias eurytheme*. Non-diapausing *Colias eurytheme* larvae require food during the autumn, winter, and early spring. Even my two apparently diapausing larvae fed into December and again by early March. Successful overwintering as pupae and eclosion when successful reproduction is possible in spring probably requires pupation in November or December in southern New Jersey[12]. No native legumes in southern New Jersey provide reliable larval food from mid October through early March, or any food at all in winter. The only evidence I have for *C. eurytheme* utilizing any native foodplants in southern New Jersey is a few ovipositions observed on *Baptisia tinctoria* (Linnaeus) R. Brown *ex* Aiton during May and June and this is also the only native foodplant noted by Shapiro (1966). Foliage of this plant is unreliable by the end of September.

Exotic cool season legumes apparently facilitated the relatively recent establishment of the orange sulphur eastward and both vetches and this butterfly seem to have arrived around the same time in southern New Jersey. Overwintering populations of *C. eurytheme* in southern New Jersey are usually associated with Eurasian vetches (*Vicia* spp.) although autumn females also oviposit on non-native white clovers (*Trifolium* spp.), which normally retain some leaves all winter. While clovers and sweet clovers (*Melilotus*), have been present in southern New Jersey for much longer, vetches were virtually absent in the early 20th century. Stone's (1911) exhaustive regional flora mentions only *Vicia tetrasperma* (Linnaeus) Schreber, describing it in a footnote as an "occasional weed". *Colias eurytheme* was still a rare stray (Smith, 1910). Moore (1989) lists five *Vicia* spp. as occasional to common in Cumberland County. *V. grandiflora* Scopoli increased dramatically in the 1990s (pers. obs.) and may now be the most common host for ovipositing spring *C. eurytheme*. According to Moore (pers. com.) a few additional vetches, including *V. tetrasperma*, are now established. Female *C. eurytheme* oviposit on at least *V. villosa* Roth and *V. grandiflora* locally. While the other five local *Vicia* species are spring annuals, *V. villosa* (=winter vetch) can grow as an annual, biennial, or perennial with growth from autumn through spring including winter (USDA, 2004). It dies back in dry summers. *V. villosa* often retains some old foliage until the first severe cold in December or January and in mild years bedraggled, but living, older leaves persist all winter. Seedlings commonly germinate in autumn under old plants, whether living or dead, and larvae could presumably transfer to these. Eggs are laid on seedlings, and established plants may put up basal growth as well. *V. villosa* presumably accounts for most or all of the abundant low vetch foliage in winter. *V. cracca* Linnaeus, a perennial, has not yet been verified locally but is widely established in eastern North America. Many successional fields have vetch foliage from late September or October into July, and all year in wet summers, and vetches are among the dominant late

[11]The lowest temperatures recorded for Atlanta, Georgia (January mean 5.8°C), Raleigh, North Carolina (mean, 4.2°C) and Millville, New Jersey (mean 0.3°C), are very similar at -22.2°C, -21.1°C, and -23.3°C respectively, but the average daily maxima for 15 January are 10.6°C, 8.9°C and 5.0°C.

[12]Based on an 8 day pupal period (Shapiro, 1967 and Gochfeld and Burger, 1997) at 24-25°C which is about the summer mean in New Jersey, at 14.5°C (the mean for 10 October) this should approximately double to 16 days and increase to approximately 25 days at 9°C (the mean for 9 November).

spring flora in these habitats. Vetches persist indefinitely in game management fields that are plowed every few years. Planted *Coronilla varia* Linnaeus patches on highway embankments usually have some tiny leaflets near ground level in mid winter (photographs in Pennsylvania from David Wright) which older larvae could probably find. There may be a period in autumn when no foliage is available but, unlike *Vicia* species, *C. varia* is a reliable foodplant all summer. Clovers are usually available from at least October to May in lawns and roadsides but die back in summer dry spells. *Melilotus officinalis* (Linnaeus) basal foliage probably is a minor winter foodplant. Shapiro (1966) and others have implicated increased cultivation of alfalfa (*Medicago sativa* Linnaeus) in the spread of the orange sulphur eastward. While post-harvest regrowth on this crop would probably be a suitable winter food, fields are usually plowed under before adults could eclose. Stone (1911) noted occasional escapes, but I have not seen alfalfa outside of cultivation locally.

The Orange Sulphur is far from unique in using alien foodplants. At least 24 (21%) of the regularly breeding butterflies and skippers in New Jersey utilize alien larval foodplants, often congenerics to native hosts (mostly personal observations). Besides both *Colias*, *Poanes viator zizaniae* Shapiro, and *Lycaena phlaea americana* Harris probably owe their current presence in this state to exotics. The now abundant *Poanes v. zizaniae* uses extremely invasive alien *Phragmites* strains, probably exclusively,[13] and last instars of the Rare Skipper (*Problema bulenta* Boisduval and LeConte) were recently found on this reed (pers. obs. with W.J. Cromartie and Marc Minno) where it was growing with the native foodplant (Cromartie and Schweitzer, 1993) in Atlantic County. An isolated population of *Hesperia attalus slossonae* Skinner in Cumberland County appears to be completely dependent on *Centaurea maculosa* (Lam.) and other exotic weeds for nectar, based on hundreds of observations by the author and Joseph Patt. Besides *Colias*, butterflies and skippers in the genera *Strymon, Cupido, Epargyreus, Thorybes*, and *Erynnis* have benefited from extensive use of non-native legumes in New Jersey. Across the continent, Graves and Shapiro (2003) report that about 34% of the butterfly and skipper species in California oviposit or feed as larvae on alien plants, although sometimes with lethal results.

[13]*P. viator* was reported by Smith (1910) and possibly originally maintained populations on then uncommon, now nearly extirpated, native *Phragmites*, but "at the edge of salt meadow" suggests the then recently established exotic. *P. viator* is scarce in the extensive wild rice marshes of the Maurice River system except near *Phragmites* patches.

Postscript. The fact that *Colias eurytheme* has within 75 years become one of the most abundant butterflies in eastern North America, suggests that interpretations of its life history being ill adapted to its new range (e.g. Scott, 1986) should be rethought. Rather I suggest a combination of lack of diapause with exceptional cold tolerance, presumably due to supercooling ability and hemolytic antifreezes (Leather et al., 1993), of larvae and pupae superbly pre-adapted this species to exploit anthropogenic habitats with cool season legumes in regions with moderately cold winters but with some warm winter days. Furthermore *C. eurytheme* has some success as a two way migrant exploiting climatically unsuitable regions to the north in the summer and returning south in autumn, though the extent of migratory ability is poorly documented. Finally, I suggest lepidopterists not ignore common species. The life history features contributing to their success might not be what one expects.

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A NOISE PRODUCING BUTTERFLY, *YPHTHIMOIDES CASTRENSIS* (NYMPHALIDAE, SATYRINAE) FROM SOUTH BRAZIL

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ABSTRACT. A new noise producing system is described for the Nymphalidae. *Yphthimoides castrensis* from south Brasil in Rio Grande do Sul, was studied to find the origin and the purpose of the sound. The noise accompanied interactions with other species of small satyrids butterflies, like *Paryphthimoides phronius* and with their own species. Illustrations of the sub-costal vein of the forewings were made to show details of the new organ in charge of this click sound, and it has been compared with the already known *Hamadryas* Vogel's organ.

Additional key words: *Paryphthimoides*, Behavior, *Hamadryas*, Vogel's organ, wing structure

INTRODUCTION

Sound production has been used by many species of animals for communication. In butterflies not many species have developed this ability, or at least they do not produce loud enough sounds for humans to hear. *Yphthimoides castrensis* (Schaus, 1902) is documented for the first time to produce sounds. Only one record of acoustic signals is documented in the satyrinae group (Kane 1982). The most studied noise producing butterfly is *Hamadryas*. Its sound is emitted because of the wing's upstroke movement, then is amplified through special veins mainly the sub-costal, which leads to a four chambered organ, called Vogel's organ (Monge-Nájera *et al.* 1998). The Vogel's organ, in the side of the butterfly body wall, is also proposed to be a hearing organ (Vogel 1912).

Y. castrensis, is often seen fling with other small butterflies like *Paryphthimoides phronius* (Godart, 1823) which belong to the Satyrinae. Many species in this sub family present a very thick area in the sub-costal vein of the forewings (DeVries, 1987), even thicker than in *Hamadryas*. The function of this structure has been unknown for many years. Seven specimens of *Y. castrensis* were studied, and the sub-costal vein of the forewings was dissected under a stereoscope. The thicker area is a little smaller than half the length of the discal cell, and it has a prominent structure like a callus, that might be the surface which is struck to produce the sound.

MATERIALS AND METHODS

Collecting in the Floresta Nacional de San Francisco de Paula in Rio Grande Do Sul (FLONA), Brazil, was done on November 2003. Collecting was done with a butterfly net between 0930 and 1400. During this time *Y. castrensis* and *P. phronius* were active and flying in low pastures areas. The specimens studied were taken to the Insects Bioecology Laboratory, in the Zoology Department of the Universidad Federal de Rio Grande do Sul. The specimens were identified, and compared with the laboratory research collection. The sub-costal vein was dissected under a stereoscope, for studying the structure of the sound organ. The wing and sound producing structures were drawn. Five more specimens of the same species from the laboratory research collection were studied and were identical in structure.

RESULTS

There are many interactions of small satyrids in the study site. Sometimes it is possible to hear a clicking noise while two, three or four of them fly together. *Y. castrensis* proved to be responsible for this sound, by catching the two species together in the net, and observing that *Y. castrensis* kept producing the sound inside the net. Each click was related to each up stroking movement of the wings, with a frequency of one click per two or three seconds, unlike *Hamadryas* where the frequency is around 2 clicks per second. This observation lasted around 10 seconds. The other species in the net, *P. phronius*, also kept doing the same movement but without producing any sound.

External structures

The sound system studied in *Y. castrensis* appears to be in the sub-costal vein (SC) of the forewings as shown in *Hamadryas* (Fig. 1), where *Y. castrensis* presents a big swelling. The widest part of the swollen area is 800 µm. more or less eight times the 100 µm. width of the base of the vein. The length of the swollen area of the vein is 6000 µm. 1/3 of the distance to the distal wing border. Close to the distal part of the swelling is a structure that seems to be a kind of spherical callus (C) with a stronger surface; this callus is 500 µm. long and

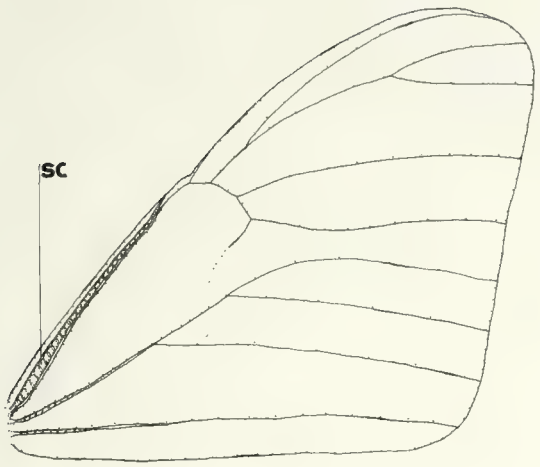

FIG. 1: Details of the sound production structures in the wing of *H. guatemalena*

300 μm. wide. The callus is at the end of the swelling; after this point the vein changes to its normal 50 μm. width. The (2A) and (3M) veins close to their origin level also presents inflation, but not as pronounced as in the (SC) (Fig. 2).

Internal Structure

The swollen area contains many small polygonal chambers of membranous walls with an irregular volume. The chamber sides are around 200 μm. The borders are weak sclerotized membranes, that might vibrate with the hitting of the callus. The volume of the swollen area was approximately 0.883 mm^3. The other partially swollen veins are not filled with individual chambers.

This complex of chambers seems to be a sound amplifier. The walls in the chambers vibrate along the structure, and the more walls that vibrate, the louder the sound might be.

The median length of the chambers walls is around 200 μm.

DISCUSSION

Apparently the sound of *Y. castrensis* is produced for communication. It is known that many animals use noise signals for different situations, like attracting mates (Wakamura 1997, Spangler *et al.* 1984), expelling territorial intruders (Alcock 1989), and to deter predators (Busnell 1963).

In the case of *Y. castrensis*, the interaction was proved to be with other species so it may have a role in territorial behavior. The host plant of these two species might be the same grass. It may be important for females and males to protect food resources against the same species, and other species. *Y. castrensis* could also use the noise to attract mates, as in *Hamadryas* (Monge-Nájera & Hernández 1991 and Monge-Nájera *et al.* 1998).

The noise production organ in *Y. castrensis* seems to be different from that studied in *Hamadryas*. *Y. castrensis* has pneumatic chambers. When hitting the callus, the independent chambers inside the organ vibrate, and each chamber helps to amplify the sound. More chambers will produce more vibration surface and louder sounds. The callus must be the structure in responsible for the first contact between the wings.

The sound structures are located in the same vein (Sc) in *Hamadryas* and in *Y. castrensis* . These similarities suggest that these structures are homologous as modifications of the veins. Otherwise, the internal structure is highly modified in the two cases, and it is

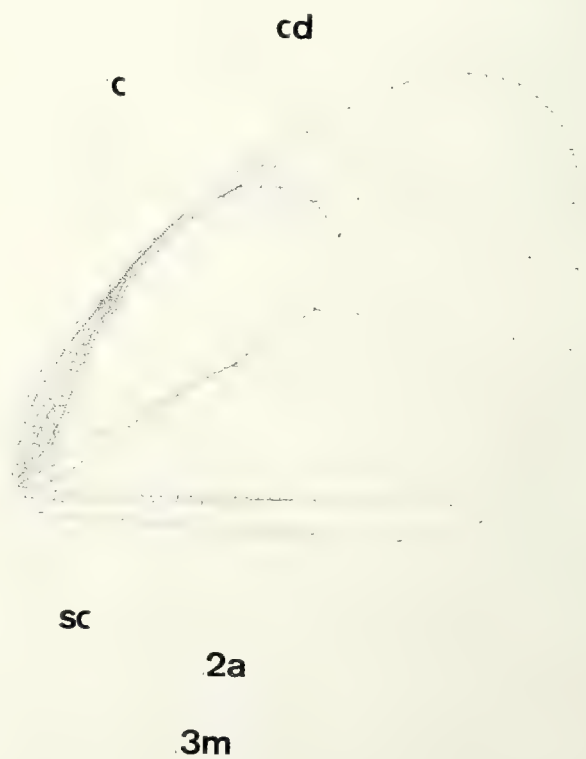

FIG. 2: Details of the sound production structures in the wing of *Y. castrensis*.

not possible to be sure if these internal structures are homologous.

In the case of *Y. castrensis* the organ is a modification of the internal membrane of the tegument of the vein. In the case of *Hamadryas* new studies are necessary about the tegument that becomes the spiral organ.

The presence of these structures suggests two possible origins: a) the sound structure develops from the vein wall; in this case the structures are examples of homoplasy or b) the sound organ in each species is a different modification with the same venal structures involved; in this case the structure may be homologous.

The phylogenetic relationships among these two species suggest the first of these possibilities.

In order to compare the effectiveness of the organ in *Y. castrensis* approximations of the (Sc) vein volume were done. The wing surface in *Hamadryas* is around three times the surface of the *Y. castrensis* wing. The volume of the *Hamadryas* (Sc) vein is around 0,041mm^3 in contrast to the *Y. castrensis* (Sc) vein, which is around 0,883 mm^3. The organ seems to be more effective in *Y. castrensis* because it is twenty one times bigger than the *Hamadryas* organ in a wing that is three times smaller, allowing it to produce a similar noise to the *Hamadryas*.

Many species of Satyrinae present this characteristic sub-costal vein, but no function has been described for it. Genera such as *Pierella, Taygetis, Chloreuptychia* and *Dioriste* could be good to compare the structures, and find out if they also produce noise; sonograms might show noises not audible to humans.

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